

ANNALS of CARNEGIE MUSEUM

THE CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 63

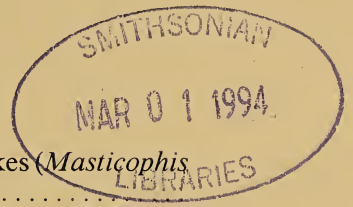
22 FEBRUARY 1994

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ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

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THE CARNEGIE
MUSEUM OF
NATURAL HISTORY

GEOGRAPHIC VARIATION AND SYSTEMATICS OF THE
STRIPED WHIPSNAKES (*MASTICOPHIS TAENIATUS* COMPLEX;
REPTILIA: SERPENTES: COLUBRIDAE)JEFFREY D. CAMPER^{1,2}JAMES R. DIXON¹

ABSTRACT

Geographic variation in morphological and protein characters in *Masticophis taeniatus* sensu lato and *Masticophis bilineatus* were investigated. Populations of striped whipsnakes in southern Texas and eastern Mexico allocated to *M. t. schotti*, *M. t. ruthveni*, and *M. t. australis* are not conspecific with those of *M. t. taeniatus* and *M. t. girardi* of the western United States and Mexico. The southeastern populations are elevated to specific status and referred to *Masticophis schotti*, whereas the western whipsnake populations remain *M. taeniatus*. Striped whipsnake populations in south-central Mexico allocated to *M. t. australis* are not separable from those making up *M. t. ruthveni* and the two taxa are synonymized. *Masticophis schotti* and *M. taeniatus* differ from one another in maxillary tooth number, preanal dorsal scale row frequency, number of apical scale pits, and color pattern. An allelic difference across the Balcones Escarpment of central Texas at the supernatant amino acid transferase (*S-Aat-A*) locus exists between *M. t. girardi* and *M. s. schotti*. *Masticophis bilineatus* shows little geographic variation. A phylogenetic analysis of geographic samples supports the monophyly of both *M. taeniatus* and *M. schotti*.

RESUMEN

Se estudió la variación geográfica de caracteres morfológicos y protéicos en *Masticophis taeniatus* sensu lato y *Masticophis bilineatus*. Las poblaciones de las culebras rayadas en el sur de Texas y este de México, ante conocidas como *M. t. schotti*, *M. t. ruthveni*, y *M. t. australis* no son conespecíficas con *M. t. taeniatus* y *M. t. girardi* del oeste de Estados Unidos y México. Las poblaciones del sureste son elevadas a la categoría de especie y referidas como *Masticophis schotti*, mientras que las poblaciones del oeste retienen el nombre de *M. taeniatus*. Las poblaciones del sur del centro de México, conocidas como *M. t. australis*, las consideramos sinonimias con *M. t. ruthveni*. Estas dos especies difieren en el número de dientes maxilares, la frecuencia de líneas de escamas dorsales preanales, el número de foetas apicales y el patrón de coloración. Existe una diferencia en el locus del supernadante del aminoácido de transferencia (*S-Aat-A*) entre *M. t. girardi* y *M. s. schotti*, localizándose sobre el Balcones Escarpment del centro de Texas. *Masticophis bilineatus* presentó poca variación geográfica. Un análisis filogenético de las muestras geográficas sostiene la monofilia de *M. taeniatus* y *M. schotti*.

INTRODUCTION

The status of populations of the striped whipsnake, *Masticophis taeniatus* sensu lato, in Texas and Mexico has long been enigmatic to herpetologists. The first name applied to snakes of this species-group was *Leptophis taeniatus* (Hallowell, 1852). Striped whipsnakes from central and western Texas and western Mexico were described as *Masticophis ornatus* (Baird and Girard, 1853). This form was subsequently recognized as a subspecies of *M. taeniatus* (Cope, 1875). Stejneger

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and Barbour (1917) did not recognize the genus *Masticophis* and relegated all species of *Masticophis* to *Coluber*. Hence they substituted *C. t. girardi* for *Coluber taeniatus ornatus*, which became a secondary junior homonym of *Coluber ornatus* Shaw, 1802 (= *Chrysopelea ornata* of Asia). Intergradation of color pattern characters between *M. t. taeniatus* and *M. t. girardi* was thought to occur in extreme western Texas (Ortenburger, 1928). Schmidt and Smith (1944) stated that the use of *Masticophis taeniatus ornatus* "appears to be in accord with the opinion of the International Commission on Zoological Nomenclature with regard to secondary homonyms." However, Article 59 of the 1985 Code stated that all secondary junior homonyms replaced before 1961 are permanently invalid; therefore, *M. t. girardi* should be used instead of *M. t. ornatus*.

Baird and Girard (1853) described *Masticophis schotti* from southern Texas, in the Tamaulipan Biotic Province. Ortenburger (1928) examined only three specimens of this taxon. Gloyd and Conant (1934) considered *M. schotti* a subspecies of *M. taeniatus*, based on two juvenile specimens that they believed to be intergrades from the eastern portion of the Edwards Plateau. A darker form with reduced striping from the lower Rio Grande valley of Texas and Tamaulipas, Mexico, described as *Masticophis ruthveni* (Ortenburger, 1923), was also considered a subspecies of *M. taeniatus* by Gloyd and Conant (1934). Based on the assumption that juvenile *M. t. ruthveni* do not have light stripes, Smith (1941) described *Masticophis taeniatus australis* from Guanajuato, Mexico.

Masticophis bilineatus was described by Jan (1863) from Mexico. Cope (1891) later applied the name *Bascanium semilineatum* to the same taxon from Arizona (Smith, 1941). Subspecies described include *Masticophis bilineatus lineolatus* (Hensley, 1950) from the Ajo Mountains of Arizona, based on minor color pattern differences, and *Masticophis bilineatus slevini* (Lowe and Norris, 1955), the putatively dwarf population on Isla San Esteban, Baja California, Mexico. Our interest in investigating geographic variation in *M. bilineatus* and the relationship of this taxon to *M. taeniatus* arose because of parapatry among similarly-patterned *M. bilineatus*, *M. t. girardi*, and *M. t. ruthveni* in south-central Mexico, and the apparent sympatry of *M. bilineatus* and *M. t. taeniatus* in central Arizona. The objectives of this study are to: (1) determine evolutionary relationships within the striped whipsnake complex, *Masticophis taeniatus sensu lato*; (2) determine evolutionary and geographic relationships between *Masticophis bilineatus* and *M. taeniatus*; and (3) document patterns of geographic variation in morphological and protein characters of *M. taeniatus* and *M. bilineatus*.

MATERIALS AND METHODS

A total of 1633 *Masticophis taeniatus* and 335 *M. bilineatus* from throughout the ranges of these species was examined (Fig. 1, Appendix 1). The states for 36 characters were recorded for each *M. taeniatus*, and 35 for each *M. bilineatus*. Four measurements (total length, tail length, head length [snout to posterior margin of the last supralabial], and greatest head width) were recorded to nearest 0.1 mm. Because the character has been used to discriminate among subspecies of *M. bilineatus* (Lowe and Norris, 1955), the length of the right posterior chin shield divided by the distance from the anterior edge of the mental scute to the posterior edge of the posterior chin shield was calculated for *M. bilineatus*. The following data were also recorded: sex; age (adult or juvenile); anal plate condition (single/divided); number of scale rows at neck, midbody, and ten ventral scutes anterior to the vent (Dowling, 1951); numbers of supralabials, infralabials, preoculars, postoculars, loreals, primary temporals, secondary temporals, ventrals, subcaudals, and maxillary teeth; and supralabials contacting the orbit. Head scale variation is presented for the right side of the head only. Fourteen color pattern characters were also recorded. Presence and width (both dorsally and laterally) of a light nuchal collar

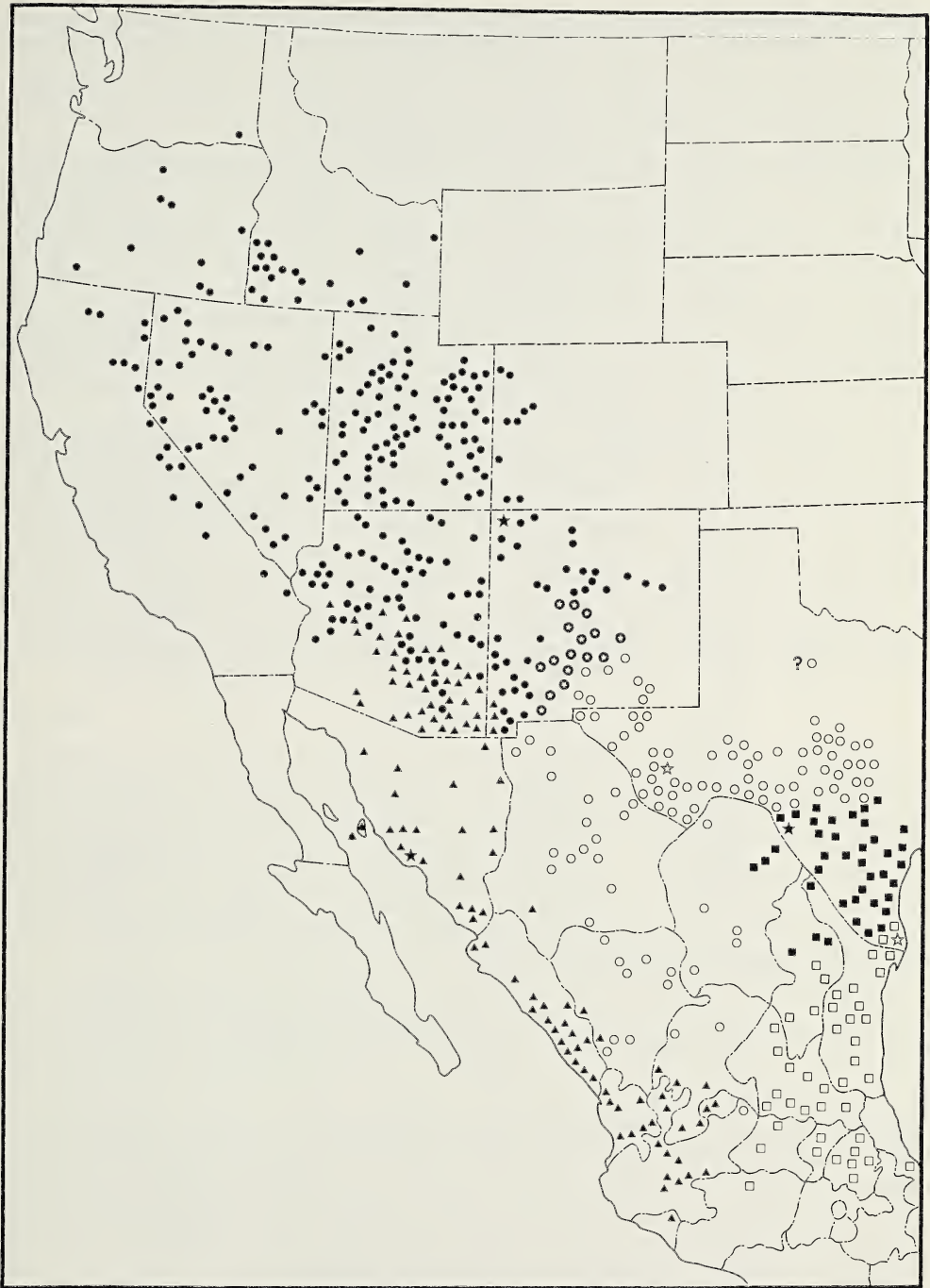


Fig. 1.—Map showing location of specimens examined in this study. Closed circles = *Masticophis t. taeniatus*, open circles = *M. t. girardi*, circled stars = *M. t. taeniatus* x *girardi*, black squares = *M. t. schotti*, open squares = *M. t. ruthveni*, and triangles = *Masticophis bilineatus*. Stars indicate type localities for respective taxa.

and number of light bands were recorded for *M. taeniatus* only. Other color pattern characters included: number of stripes; stripe color (light or dark); stripe position (scale row location); presence of dorsal speckling; presence of light head scale borders; dorsal color pattern; ventral pattern of neck, belly, and tail; and length of stripes expressed in numbers of ventral scutes. Scale row reductions were recorded for each specimen and presented in the formula recommended by Dowling (1951). The length of the inverted hemipenis was recorded in terms of subcaudals subtended.

Measurements were used to calculate five ratios: tail length/snout-vent length (TLR), head length/head width (HR), head length/snout-vent length (HLSVL), head width/snout-vent length (HWSVL), and posterior chin shield/mental-posterior chin shield distance (CSR, *M. bilineatus* only). Tests of geographic variation used analysis of variance (ANOVA) and Duncan's multiple range (univariate) and canonical discriminant analyses (multivariate) employing the GLM and CANDISC procedures of the Statistical Analysis System software package, respectively (SAS Institute, 1985). A significance level of $\alpha = 0.05$ was used on all statistical tests. Phenograms based on distance and correlation coefficient matrices were generated with the unweighted pair-group method using arithmetic means (UPGMA) algorithm of the Numerical Taxonomy System of Multivariate Statistical Programs, NTSYS (Rohlf et al., 1980). Version 2.4 of Phylogenetic Analysis Using Parsimony (PAUP) and the associated CONTREE were used to perform phylogenetic analyses (Swofford, 1985). Genotype data were analyzed with Biosys-I computer software (Swofford and Selander, 1981).

Sexual, phylogenetic, and geographic variation analyses were conducted on the 22 samples shown in Fig. 3. Samples 1–17 and 22 represent *M. taeniatus* sensu lato and 18–21 are *M. bilineatus*. Samples included mapped localities grouped in 80.5 km² unit areas delineated after examining the geographic distribution of locality data and considering major biogeographic boundaries. Cluster analysis of the 80.5 km² unit areas, using the UPGMA algorithm on separate sexes, yielded these 22 samples (Fig. 3).

Heart, liver, kidney, and skeletal muscle tissue removed from freshly sacrificed specimens of *M. taeniatus* sensu lato (33), and *M. bilineatus* (3) were used to analyze protein variation by horizontal starch gel electrophoresis (Harris and Hopkinson, 1976; Selander et al., 1971; Table 1). Data from *M. bilineatus* were not included in analyses because too few individuals were available to accurately estimate allozyme variation. Voucher specimens are deposited in the Texas Cooperative Wildlife Collections, University of Texas at El Paso, and New Mexico State University (Appendix 2).

RESULTS

Ontogenetic Variation.—Due to insufficient samples of juveniles, the description of ontogenetic variation is limited to color pattern differences between adults and hatchlings. The hatchling color pattern of *M. taeniatus* sensu lato is invariable throughout its range (Fig. 2). The holotype of *M. t. australis* also exhibited this pattern and is identical to all other juvenile specimens examined. Adult color patterns are shown in Fig. 13 (*taeniatus*), 15 (*girardi*), 17 (*schotti*), and 19 (*ruthveni*). The color pattern of *M. bilineatus* changes little ontogenetically; therefore, only adult color patterns are shown (Fig. 20).

Hatchling *M. taeniatus* have a ground color of dark olive green dorsally, with two white or cream lateral stripes. One stripe encompasses the lower half of scale row 1 and the lateral edges of the ventrals. The other stripe is on the upper half of scale row 3 and the lower half of scale row 4. The dorsal pattern is most similar to that of adult *M. t. schotti* or some *M. t. ruthveni*, differing only in ground color shade and absence of dorsal speckling. Hatchlings have a cream-colored venter with a narrow, diffuse dark olive lateral stripe forming the lower border of the lower light stripe. The medial portion of the venter is immaculate. Some hatchling *M. taeniatus* have paired black spots on the first five to ten ventral scutes. Spots may also be scattered on the chin shields and gular scales. Hatchlings are most similar to adult *M. t. taeniatus* in ventral color pattern.

Sexual Variation.—Eleven characters and snout-vent length (SVL) were tested for sexual variation (Table 2). Samples 4, 11, 15, 16 (*M. taeniatus*), and 18 (*M. bilineatus*) were chosen because they are the largest (Fig. 3). A lower limit of 500 mm SVL was chosen for adult size in analyses of SVL. Males had significantly larger body sizes than females in samples 11 and 18 (Table 2).

Table 1.—*Proteins examined, tissues of origin, and electrophoretic conditions yielding best resolution of Masticophis taeniatus allozymes. Mitochondrial and supernatant loci are denoted by M- and S- prefixes, respectively.*

Protein	Enzyme Commission number	Locus	Tissue	Electrophoretic conditions ^a
Aminopeptidase	3.4.11.1	<i>AP-A</i>	liver	A
Aspartate aminotransferase	2.6.1.1	<i>M-AAT-A</i>	liver	B
	2.6.1.1	<i>S-AAT-A</i>	liver	C
Creatine kinase	2.7.3.2	<i>CK-A</i>	muscle	D
	2.7.3.2	<i>CK-C</i>	muscle	C
Dihydrolipoamide dehydrogenase	1.8.1.4	<i>DDH-A</i>	liver	B
Esterase ^b		<i>EST-D</i>	liver	C
Fumarate hydratase	4.2.1.2	<i>FUMH-A</i>	liver	C
General protein		<i>GP-1</i>	muscle	C
Glucose-6-phosphate dehydrogenase	1.1.1.49	<i>G6PDH-A</i>	heart	C
Glutamate dehydrogenase	1.4.1.2	<i>GTDHP-A</i>	liver	C
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	<i>GAPDH-A</i>	muscle	C
Isocitrate dehydrogenase	1.1.1.42	<i>M-IDH-A</i>	liver	C
	1.1.1.42	<i>S-IDH-A</i>	liver	C
Lactate dehydrogenase	1.1.1.27	<i>LDH-A</i>	liver	C
	1.1.1.27	<i>LDH-B</i>	liver	C
Malate dehydrogenase	1.1.1.37	<i>M-MDH-A</i>	liver	C
	1.1.1.37	<i>S-MDH-A</i>	liver	C
Mannose-6-phosphate isomerase	5.3.1.8	<i>MPI-A</i>	muscle	D
Peptidase ^c	3.4.-.-	<i>PEP-A</i>	liver	A
		<i>PEP-B</i>	liver	A
		<i>PEP-C</i>	liver	A
		<i>PEP-S</i>	liver	A
Phosphoglucomutase	5.4.2.2	<i>PGM-A</i>	muscle	C
	5.4.2.2	<i>PGM-B</i>	muscle	C
Proline dipeptidase	3.4.13.9	<i>PRO-A</i>	liver	A
Pyruvate kinase	2.7.1.40	<i>PK-A</i>	liver	C
Superoxide dismutase	1.15.1.1	<i>S-SOD-A</i>	liver	B
Xanthine dehydrogenase	1.1.1.204	<i>XDH-A</i>	liver	B

^a A: Tris-HCl pH 8.5/borate pH 8.2; B: Discontinuous tris-citrate-borate (Poulik, 1957); C: Tris-citrate pH 8.0; D: Tris-citrate pH 7.0.

^b The substrate used was methyl-umbelliferyl acetate.

^c Substrates used were leucyl-alanine for Peptidase A and C, leucyl-glycyl-glycine for Peptidase B, and leucyl-leucyl-leucine for Peptidase S.

Mean ventral counts were greater for females in samples 15 and 16, and greater for males in sample 18 (Table 2). Males had significantly higher mean subcaudal counts than females (Table 2). Males in samples 11 and 15 had greater mean maxillary tooth counts than females. Males had relatively longer tails, as measured by TLR, in sample 11, whereas females had relatively longer tails in sample 15 (Table 2). Sexual variation was not found in HR, HLSVL, or HWSVL. Males in samples 11 and 15 had relatively longer heads (Table 2).

Males in samples 4, 11, 15, and 16 had significantly fewer posterior scale rows than females. *Masticophis taeniatus* sensu lato always has 15 scale rows anteriorly and at midbody. The first scale row reduction (SRR1) is lateral (scale row 3) and paired. Therefore, SRR1 reduces scale rows from 15 to 13, and is considered a

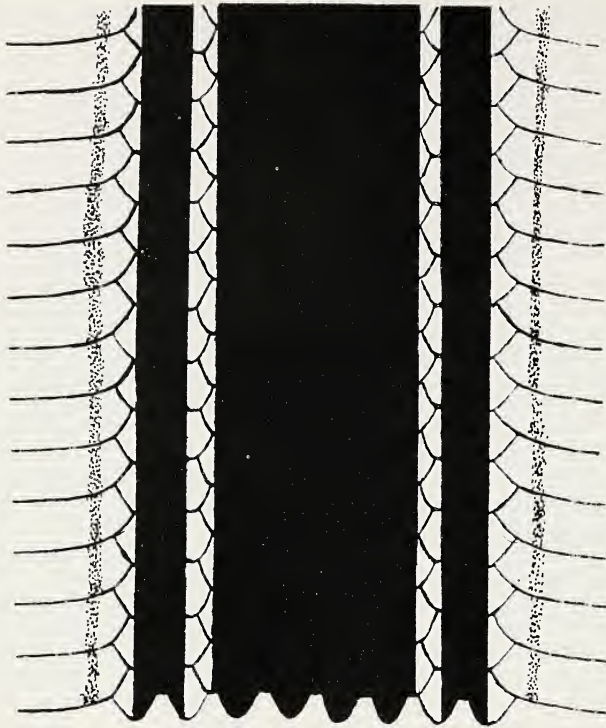


Fig. 2.—Color pattern of juvenile *Masticophis taeniatus* sensu lato.

single reduction site. The second (SRR2) and third (SRR3) reduction sites are unpaired, located middorsally, and occur separately. Most males in samples 4 (85%) and 11 (68%) had three scale row reduction sites (15-15-11, Table 2), whereas most females in these samples (80% and 69%, respectively) had two scale row reduction sites (15-15-12). Most males in samples 15 (57%) and 16 (48%) had two (15-15-12) scale row reductions (Table 2), whereas most females in samples 15 (75%) and 16 (84%) had one scale row reduction site (15-15-13). This is also illustrated by the small number of females in samples 15 and 16 with more than one scale row reduction site (Table 2). Females have a greater relative girth posteriorly as indicated by the more posteriad location of scale row reduction sites. The locations of all reduction sites were significantly different between the sexes in sample 11, but only SRR2 was significantly different in sample 4 (Table 2).

Virtually all *M. bilineatus* possess 17-17-13 scale rows. Scale row reduction 1 occurs laterally and is paired on scale row 4. The location of SRR2 and SRR3 were significantly different between the sexes in sample 18 (Table 2). Unlike the other four samples (*M. taeniatus*), males in sample 18 had SRR2 and SRR3 significantly more posteriad than did females.

Geographic Variation.—Geographic variation in ventral and subcaudal scutes was analyzed by plotting sample statistics on modified Dice-Leraas diagrams (Fig. 4-7). Samples with nonoverlapping shaded boxes (± 2 SE) have means that are significantly different. Males in samples 15-17, 20, and 21 had significantly fewer mean ventrals than most in samples 1-14, 18, and 19 (Fig. 4). In females, samples

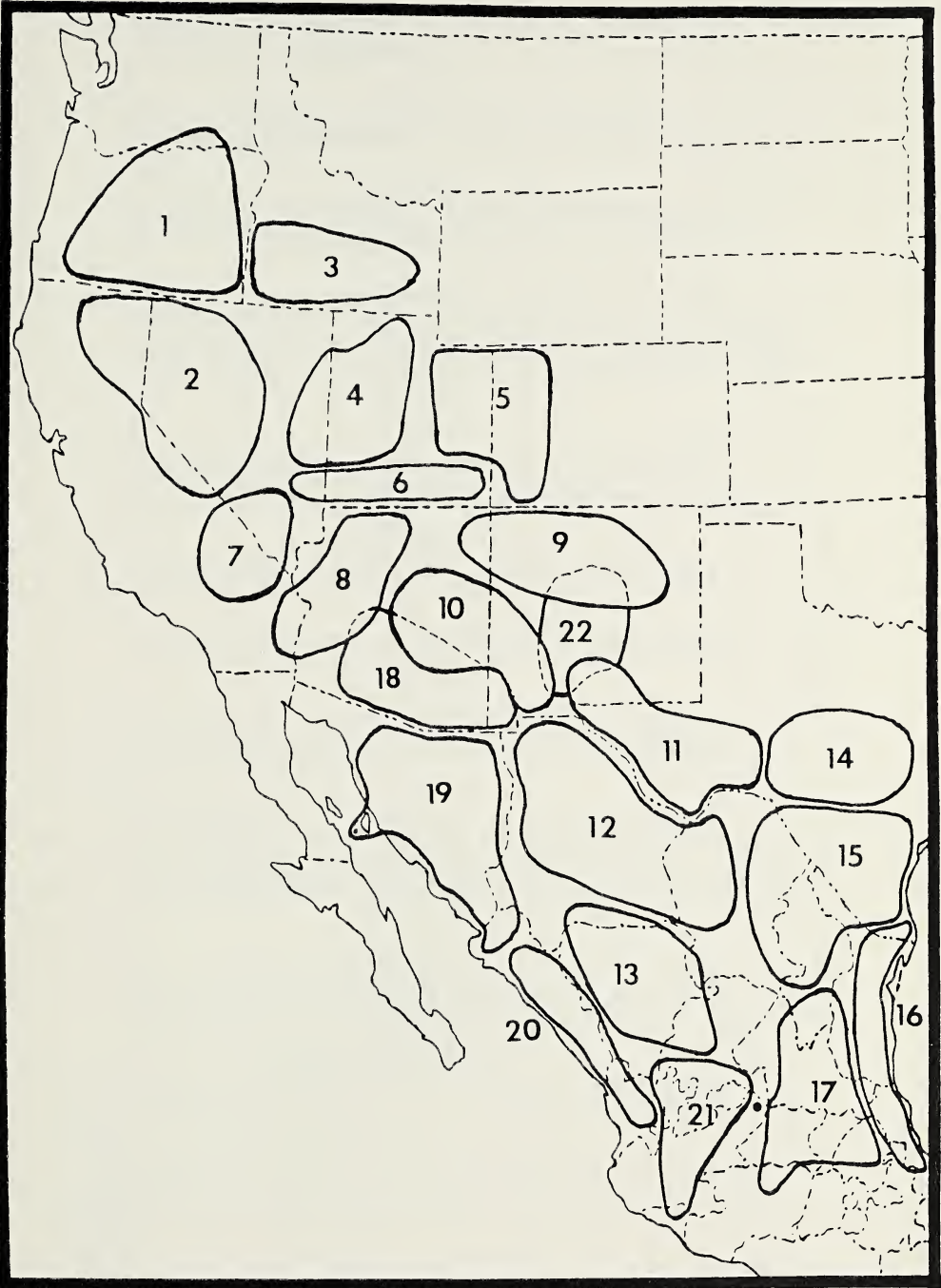


Fig. 3.—Distribution and location of the 22 samples of *Masticophis* used in this study. The locality between samples 17 and 21 is in sample 13 and is represented by one specimen only.

Table 2.—Statistically significant ($\alpha = 0.05$) sexual variation in samples 4, 11, 15, 16, and 18.

Character	Sample	Males				Females				
		\bar{x} (SD)	Range	SE	n	\bar{x} (SD)	Range	SE	n	t
SVL ^a	11	930 (160.56)	511–1214	12.9	154	861 (143.25)	513–1166	14.3	101	3.58
Ventrals ^a	18	957 (173.09)	537–1353	18.8	85	870 (141.38)	356–1155	15.2	86	3.59
	15	196 (4.51)	181–206	0.53	72	200 (5.74)	188–213	0.80	52	–4.10
	16	193 (4.77)	183–203	0.76	39	196 (7.65)	184–213	1.53	25	–2.40
SC ^a	4	138 (8.46)	120–165	1.16	53	131 (7.63)	120–145	0.85	44	4.51
	11	150 (10.2)	131–175	0.97	112	147 (11.0)	105–178	1.41	61	2.12
	15	143 (8.93)	120–162	1.32	46	138 (9.79)	119–162	1.79	30	2.17
Maxillary teeth ^b	16	143 (10.5)	129–160	2.61	16	135 (9.72)	113–152	2.81	12	2.07
	18	143 (9.58)	124–167	1.48	42	139 (8.06)	124–165	1.42	32	2.05
	11	19.2 (1.02)	15–23	0.09	140	18.8 (0.90)	16–21	0.10	89	1.97
TLR ^b	15	17.4 (0.79)	16–19	0.10	69	17.3 (0.94)	16–20	0.14	48	1.98
	11	0.455 (0.107)	0.188–0.775	0.007	125	0.451 (0.081)	0.126–0.647	0.009	82	1.97
	15	0.453 (0.064)	0.180–0.572	0.007	88	0.430 (0.069)	0.228–0.517	0.009	61	1.98
HLSVL ^b	11	0.029 (0.002)	0.027–0.041	0.00	131	0.030 (0.003)	0.015–0.035	0.00	80	1.97
	15	0.033 (0.006)	0.018–0.051	0.001	76	0.032 (0.047)	0.026–0.050	0.001	53	1.98
	4	11.1 (0.44)	9–12	0.05	72	11.8 (0.42)	11–13	0.05	61	1.98
Prenatal scale rows ^b	11	11.2 (0.54)	10–12	0.04	151	11.8 (0.51)	11–13	0.05	94	1.97
	15	11.8 (0.62)	11–13	0.07	76	12.7 (0.49)	11–13	0.07	55	1.98
	16	11.8 (0.70)	11–13	0.11	40	12.8 (0.50)	11–13	0.10	24	2.00
SRR1 ^a	11	123 (7.55)	101–145	0.63	145	125 (6.53)	110–140	0.68	93	–2.50
SRR2 ^a	4	128 (7.83)	110–154	0.92	72	136 (10.6)	116–173	1.40	58	–5.10
	11	131 (9.37)	110–158	0.78	145	139 (11.8)	119–180	1.27	86	–5.80
	18	124 (9.95)	91–167	1.11	84	121 (8.79)	93–154	1.00	82	2.12
SRR3 ^a	11	160 (13.2)	127–195	1.30	103	166 (13.5)	139–187	2.70	25	–1.90
	18	135 (18.7)	113–192	2.41	60	127 (12.6)	95–189	1.55	66	2.91

^a Student's *t* test on raw data.^b Wilcoxon Rank Sum test on raw data.

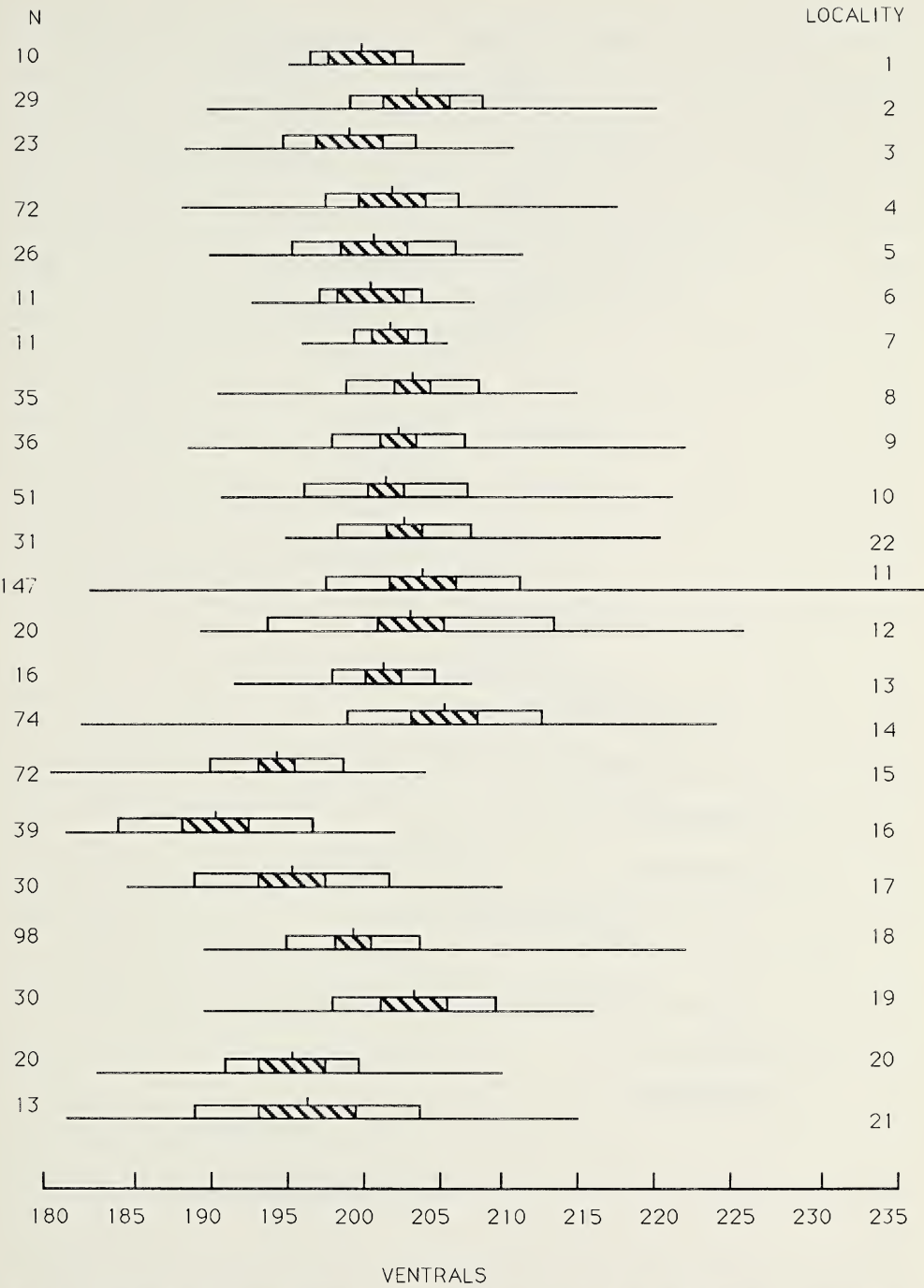


Fig. 4.—Modified Dice-Leraas diagram of geographic variation in ventrals of males of samples 1–22 shown in Fig. 3. Horizontal line is range, vertical line is mean, clear box is ± 1 SD, and shaded box is ± 2 SE.

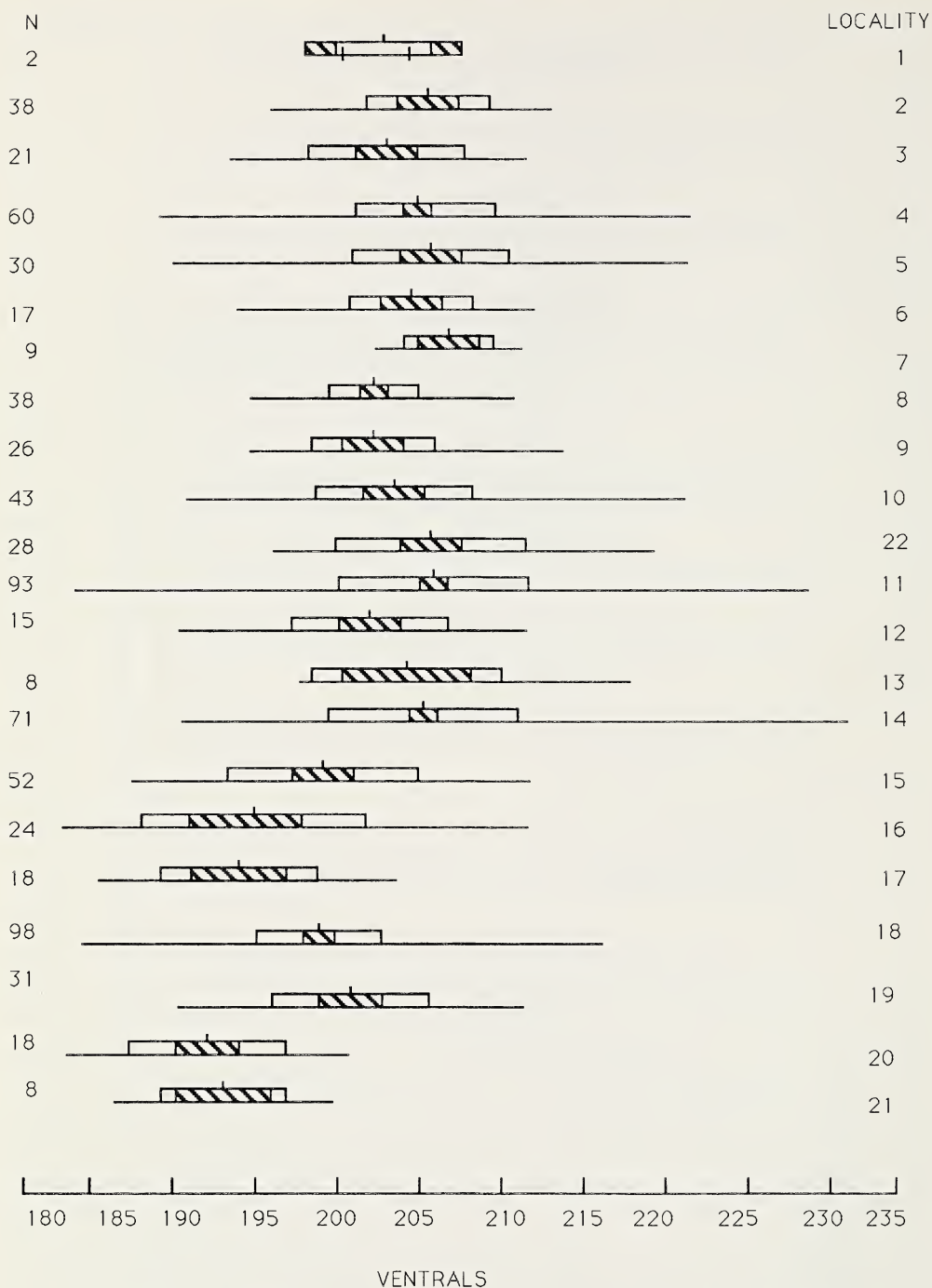


Fig. 5.—Modified Dice-Leraas diagram of geographic variation in ventrals of females of samples 1–22 shown in Fig. 3. Explanation as in Fig. 4.

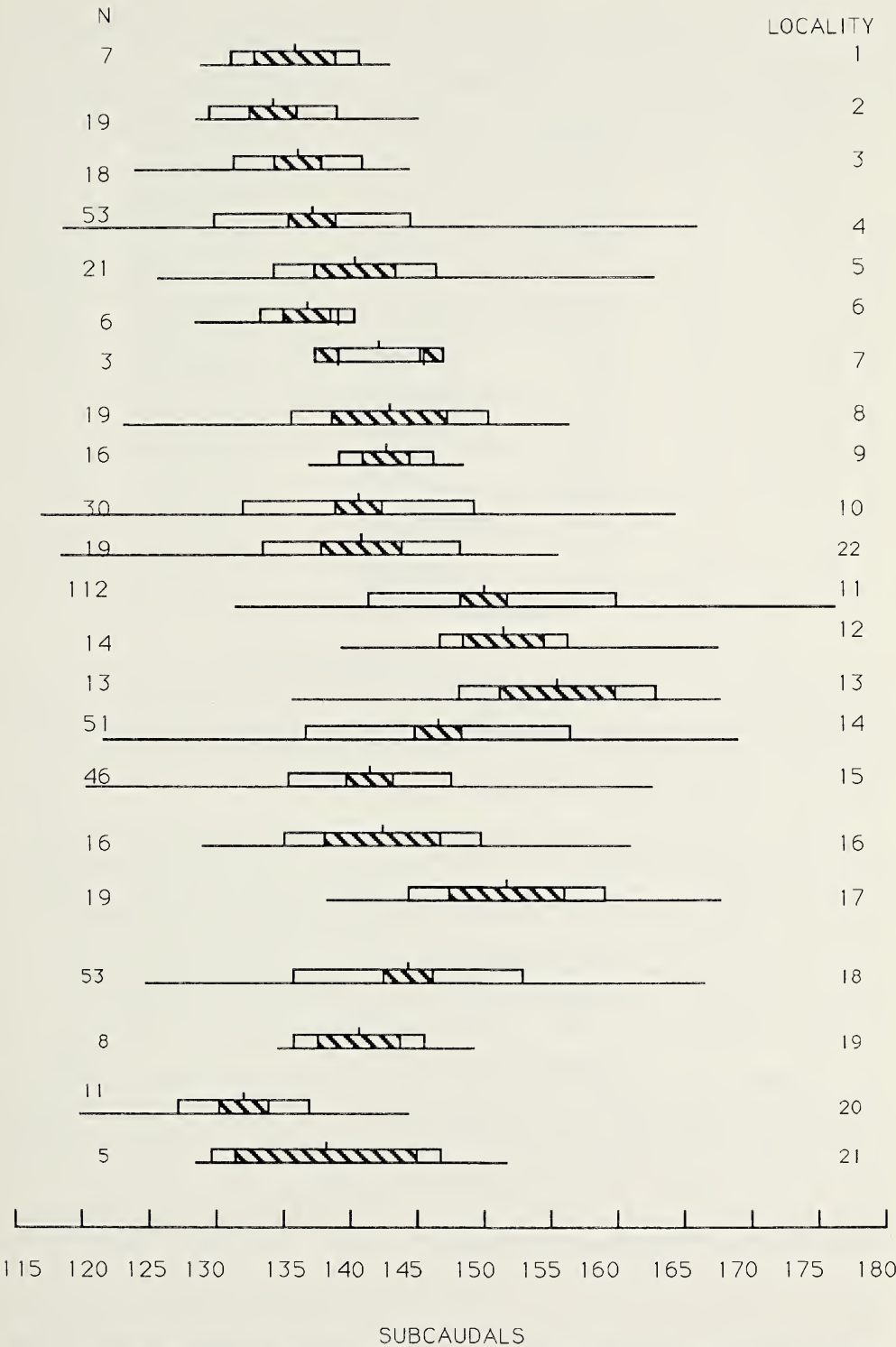


Fig. 6.—Modified Dice-Leraas diagram of geographic variation in subcaudals of males of samples 1–22 shown in Fig. 3. Explanation as in Fig. 4.

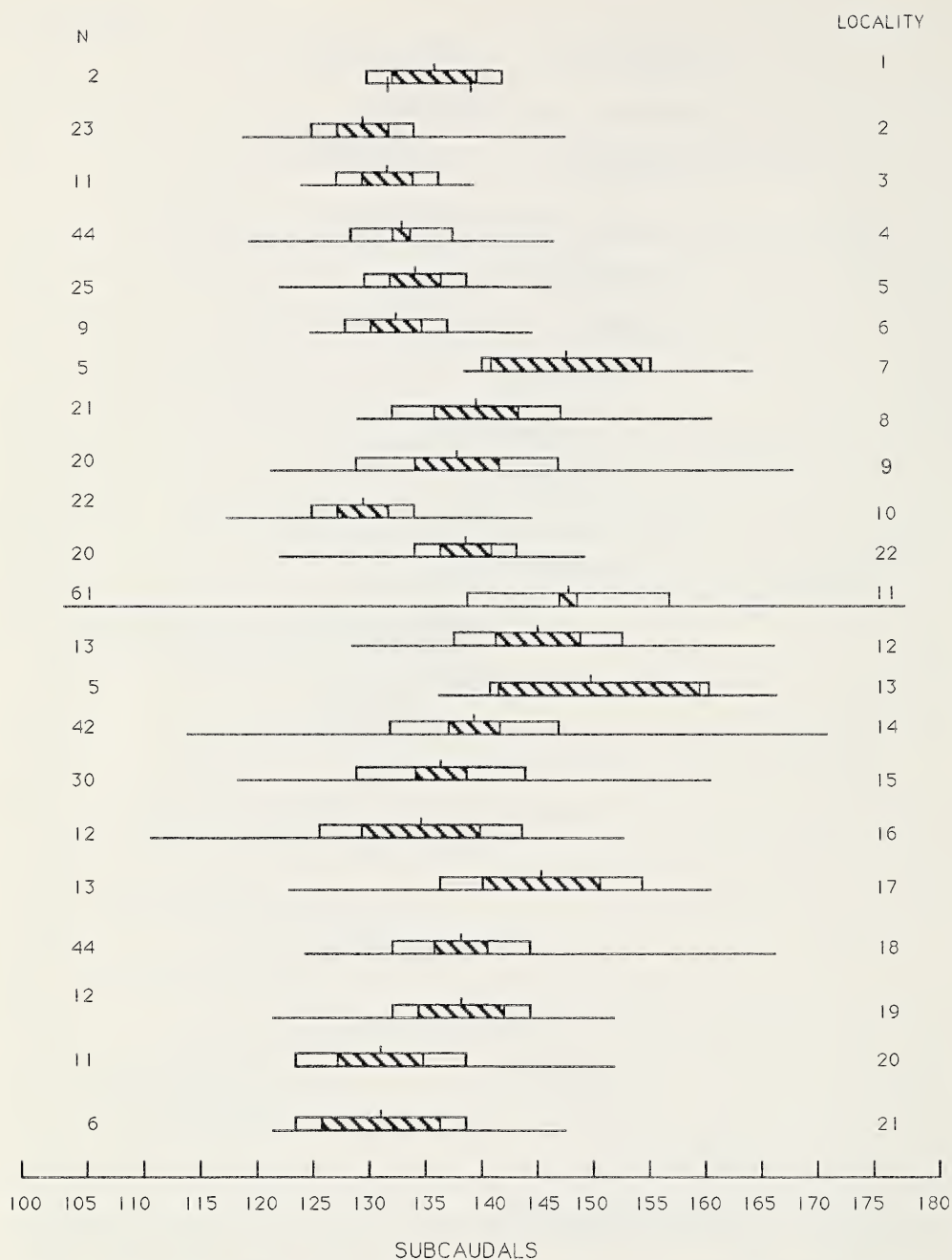


Fig. 7.—Modified Dice-Leraas diagram of geographic variation in subcaudals of females of samples 1-22 shown in Fig. 3. Explanation as in Fig. 4.

Table 3.—Geographic variation in HLSVL among samples 1–22 shown in Fig. 3. Means of samples grouped by the same letter are not significantly different.

<i>n</i>	\bar{x} (SD)	Range	SE	Sample	Grouping
34	0.034 (0.002)	0.030–0.037	0.000	20	B
33	0.033 (0.002)	0.029–0.036	0.000	17	C
10	0.033 (0.002)	0.030–0.036	0.001	21	C
164	0.033 (0.002)	0.021–0.040	0.000	18	C
55	0.033 (0.003)	0.029–0.048	0.000	19	C
30	0.032 (0.002)	0.030–0.038	0.000	16	C F
20	0.031 (0.002)	0.028–0.035	0.000	13	D F
63	0.031 (0.002)	0.023–0.041	0.000	10	D F
28	0.031 (0.002)	0.027–0.039	0.000	12	A D F
60	0.030 (0.002)	0.025–0.036	0.000	8	A D E F
55	0.030 (0.003)	0.027–0.049	0.000	5	A D E F
35	0.030 (0.002)	0.018–0.037	0.000	15	A D E F
48	0.030 (0.002)	0.026–0.036	0.000	9	A D E F
19	0.030 (0.002)	0.028–0.034	0.001	7	A D E F
32	0.030 (0.002)	0.027–0.035	0.000	3	A D E F
56	0.030 (0.002)	0.027–0.035	0.001	22	A D E F
120	0.030 (0.002)	0.025–0.035	0.000	4	A D E F
60	0.030 (0.002)	0.027–0.035	0.000	2	A D E F
145	0.029 (0.002)	0.015–0.035	0.000	11	A E F
12	0.029 (0.001)	0.028–0.032	0.000	1	A E F
97	0.029 (0.004)	0.023–0.058	0.000	14	A E
27	0.029 (0.003)	0.018–0.034	0.001	6	E

16, 17, 20, and 21 had significantly fewer mean ventrals than most other samples (Fig. 5). However, ranges overlap extensively for both sexes. In both sexes there were significant differences in mean ventral counts between parapatric samples 14 and 15. The boundary between sample 14 (*girardi*) and sample 15 (*schotti*) forms the only contact zone between these taxa that is well-represented by specimens.

An increase in average subcaudal number in southern populations of males was evident among samples 1–13 and 15–17 (Fig. 6). A significant difference in mean subcaudal counts between samples 14 and 15 existed (Fig. 6). Sample 20 had a significantly lower mean subcaudal count than all other samples except 1, 2, and 21. A northwest to southeast clinal increase in subcaudals was present in females of samples 1–10 (Fig. 3, 7). Females in sample 22 (*M. t. taeniatus* × *M. t. girardi*) were intermediate between sample 10 (*taeniatus*) and sample 11 (*girardi*). A north to south clinal decrease in subcaudal number was evident among females in samples 14–16 and 18–21 (Fig. 3, 7).

ANOVAs were significant for hemipenis length, maxillary tooth counts, TLR, HR, HLSVL, and HWSVL. However, Duncan's multiple range tests showed significant variation in HLSVL only. Sample 20 had a significantly larger mean HLSVL ($P < 0.05$, d.f. = 1254, $n = 1255$). Samples grouped by the same letters have means that are not significantly different (Table 3). Samples 1–4, 15, and 17 had the largest mean hemipenis lengths; however, no significant groupings were found ($P < 0.05$, d.f. = 447, $n = 448$). Average maxillary tooth counts for samples 11–14 and 18–21 were greater than those for samples 1–10 and 15–17; however, no significant groupings were found ($P < 0.05$, d.f. = 693, $n = 694$). Samples 9, 11–13, and 16–17 had proportionately the longest tails, averaging >47% of SVL, whereas samples 1–4 had the lowest TLR values with averages

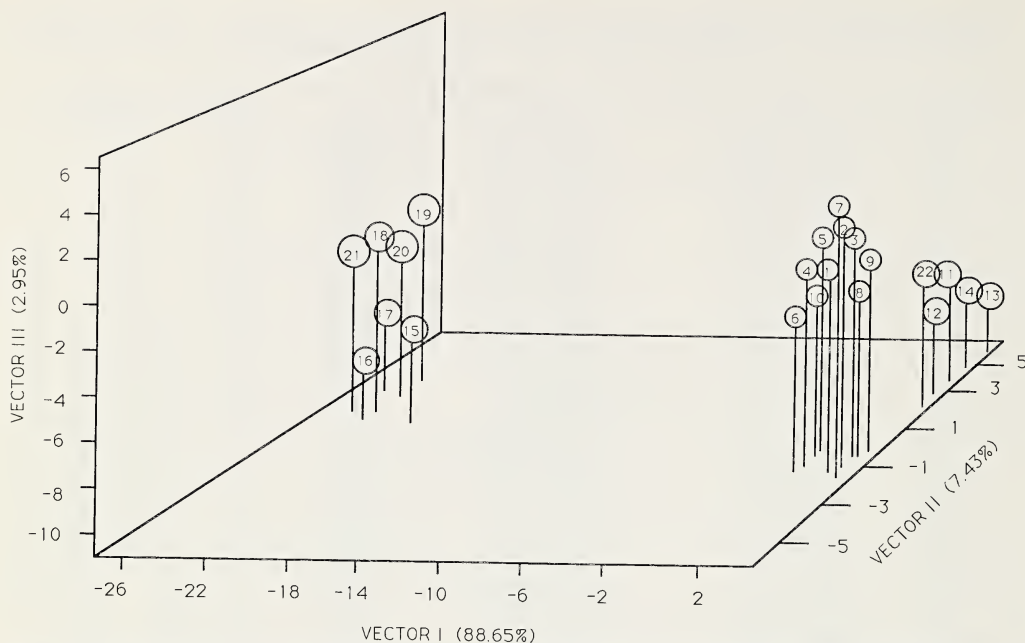


Fig. 8.—Projections on the first three canonical vectors of sample means of 22 samples of male striped whipsnakes, *Masticophis*.

$\leq 44\%$ of SVL. However, no significant groupings were found ($P < 0.05$, d.f. = 877, $n = 878$). No significant groupings of samples based on mean HR were found ($P < 0.05$, d.f. = 1252, $n = 1253$). Relative head width as measured by HWSVL was greater in southern samples, but no significant groupings were found ($P < 0.05$, d.f. = 1250, $n = 1251$).

Lowe and Norris (1955) implied that a lower CSR was characteristic of the insular and Ajo Mountains populations of *M. bilineatus*. Kruskal-Wallis tests comparing the Ajo Mountains population with four southern Arizona populations and southwestern New Mexico material were significant ($X^2 = 11.76$, $P < 0.05$, d.f. = 3). However, a Duncan's multiple range test comparing means of these populations showed no significant differences. A Kruskal-Wallis test showed no significant variation in CSR among samples 18–21 ($X^2 = 5.08$, $P > 0.05$, d.f. = 3). The population of *M. bilineatus* from Isla San Esteban did not differ significantly in SVL from three mainland Sonora populations (Kruskal-Wallis test, $X^2 = 3.02$, $P > 0.05$, d.f. = 3). The insular specimens were not significantly smaller, $t' = 0.981$, d.f. = 266, $P > 0.05$, with mean SVLs of 899 mm for 254 mainland adults and 854 mm for 14 adults from Isla San Esteban.

Multivariate analyses utilized the following characters: scale pit number, preanal scale rows, ventral counts, TLR, number of transverse light bands, number of stripes, maxillary tooth counts, HR, HLSVL, HWSVL, SRR1, and SRR2. A canonical discriminant analysis using Wilk's Lambda, Pillai's Trace, Hotelling-Lawley's Trace, and Roy's Greatest Root was conducted to test the null hypothesis of no overall significant variation due to locality. All were significant at $P < 0.05$. In the canonical discriminant analysis, canonical vectors I–III explained most (99.03%) of the variation (Table 4). Samples 1–14 and 22 separated from samples

Table 4.—*Eigenvalues and percent influence for 12 canonical vectors for the 22 samples of male striped whipsnakes, Masticophis shown in Fig. 3.*

Canonical vector	Eigenvalue	Percent influence	Cumulative
I	75.5058	88.65	88.65
II	6.3298	7.43	96.08
III	2.5133	2.95	99.03
IV	0.2564	0.30	99.33
V	0.1852	0.22	99.55
VI	0.1440	0.17	99.72
VII	0.0849	0.10	99.82
VIII	0.0487	0.06	99.88
IX	0.0442	0.05	99.93
X	0.0252	0.03	99.96
XI	0.0196	0.02	99.98
XII	0.0152	0.02	100.00

15–21 along canonical vector I which summarized 88.65% of the variation (Fig. 8; Table 4). Number of stripes was the most influential character along this axis (Table 5). Canonical vector II accounted for 7.43% of the variation and separated samples 1–10 from 11–14 and 22. Band number influenced this axis greatly (Table 5). Canonical vector III accounted for 2.95% of the variation and separated samples 15–17 from 18–21 (Fig. 8). Preanal dorsal scale row counts and SRR2 position influenced this vector the most (Table 5).

The patterns of separation seen in the canonical discriminant analysis were concordant with cluster analysis (Fig. 9). Characters used in cluster analysis included: scale pit number, number of scale rows around the anterior body, preanal scale rows, ventral counts, subcaudal counts, hemipenis length, number of transverse bands, number of stripes, maxillary tooth counts, TLR, HR, HLSVL, HWSVL, SRR1, SRR2, and SRR3. Three distinct clusters separating at distance values >1.0 were found (Fig. 9). Samples 1–14 and 22 form the largest cluster, with samples 15–17 and 18–21 forming two smaller clusters, respectively. Western samples 1, 2, and 7 grouped together, sample 22 grouped with the geographically proximate samples 9–10, but not with 11 or 12 (Fig. 3, 9). The significance of the relative position of sample 6 to samples 1–10 and the split among samples 11–14 is unclear, especially since neither were separated in Fig. 8.

Table 5.—*Variable coefficients for canonical variates I–III for 22 samples of male striped whipsnakes, Masticophis.*

Character	Vector I	Vector II	Vector III
Scale pit	0.1428	0.0817	0.1390
Preanal scale rows	−0.3550	0.1028	1.1623
Ventrals	0.0361	−0.0169	0.4014
TLR	−0.0304	0.0374	−0.2538
Bands	0.0732	2.6390	−0.1375
Stripes	8.2383	−0.9094	0.5162
Maxillary teeth	0.0420	0.2498	0.4193
HR	0.0460	−0.0912	0.0365
SRR1	−0.1404	0.1409	0.2080
SRR2	0.1767	−0.0922	−1.3304
HLSVL	0.0341	−0.0474	0.1031
HWSVL	0.0326	0.0412	−0.0650

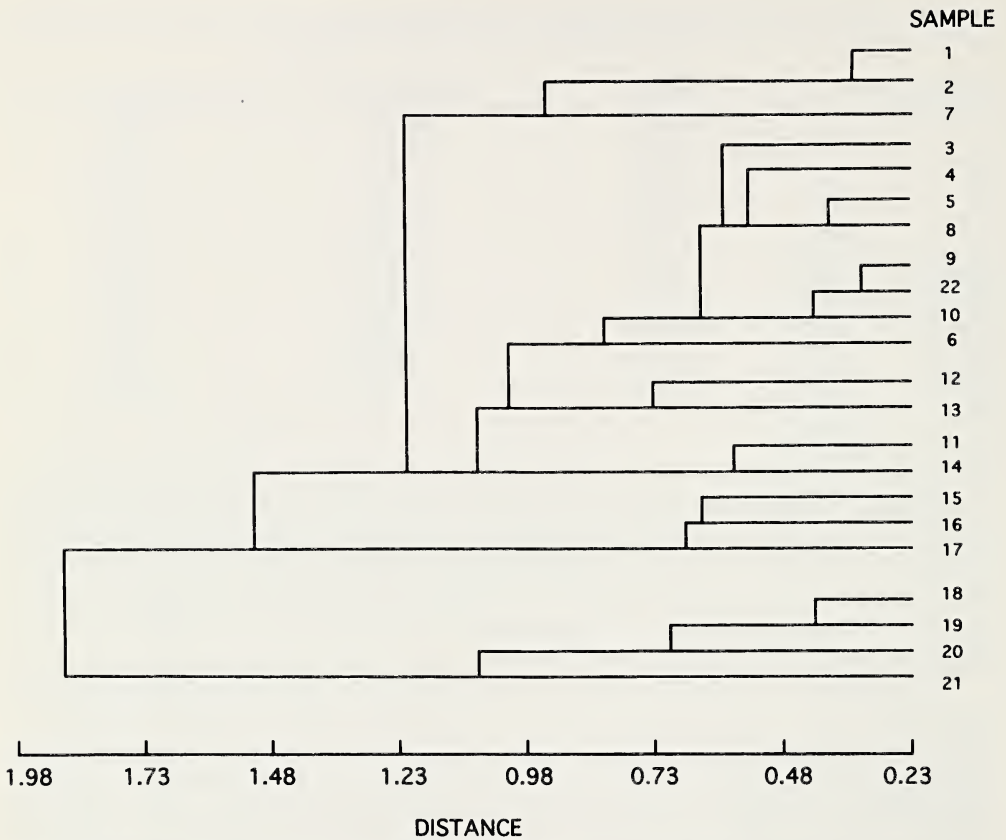


Fig. 9.—Phenogram based on UPGMA clustering of 16 morphological characters among 22 samples of male striped whipsnakes, *Masticophis*. Cophenetic correlation = 0.921.

A phylogenetic analysis based on the number of scale rows around the anterior body, preanal scale rows, number of transverse bands, number of stripes, scale pit number, dorsal speckling, head scale bordering, maxillary tooth counts, ventral counts, subcaudal counts, hemipenis length, and stripe color yielded the consensus tree shown in Fig. 10. Samples 18–21 were used for outgroup rooting. The mulpars option of PAUP version 2.4 produced nine most parsimonious trees 19 steps long with a consistency index of 0.842. Two monophyletic groups are evident, one consisting of samples 1–14 and 22 and another containing samples 15–17. Placement of samples within these groups and within the outgroup may not represent an accurate phylogenetic hypothesis due to the high probability of reticulate evolution among samples within groups (Thorpe, 1987). This tree differs from the phenogram (Fig. 9) in that sample 22 was placed with samples 11–14 and not samples 6 and 10. Otherwise the phylogenetic tree (Fig. 10) and the phenogram (Fig. 9) have similar topologies. The presence of 15 dorsal scale rows around the anterior body and at midbody is a synapomorphy uniting samples 1–17 and 22 within the *M. taeniatus* complex. Samples 18–21 have the plesiomorphic condition of 17 scale rows around anterior and midbody.

Allozyme Variation.—The protein products of 29 presumptive gene loci were

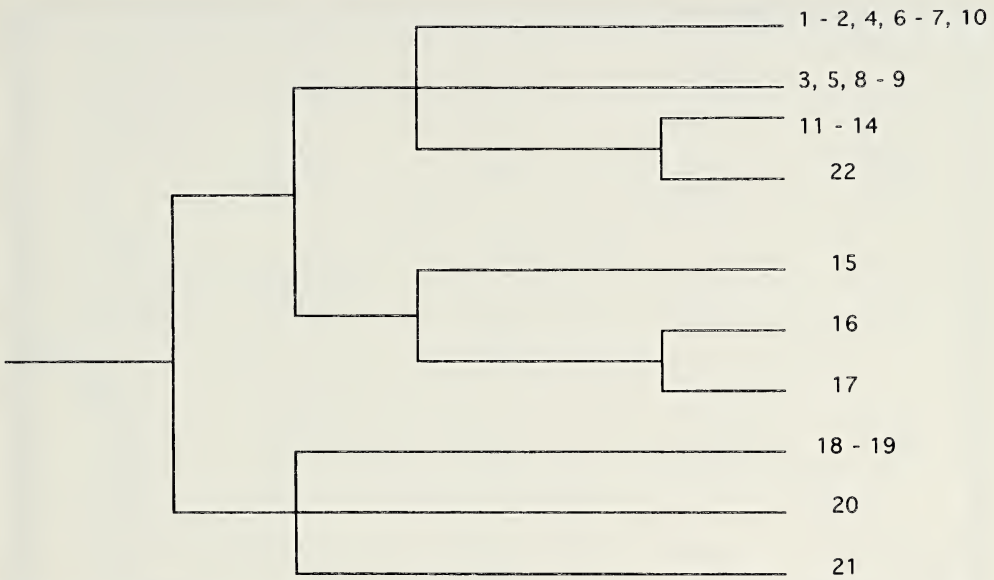


Fig. 10.—Phylogenetic tree of 22 samples of *Masticophis* shown in Fig. 3. Consistency index = 0.842.

assayed for variation in *M. taeniatus* sensu lato. Twelve of the 29 loci were polymorphic (Table 6). *Masticophis t. girardi* exhibited polymorphism at ten of the 12 variable loci. *Masticophis t. girardi* and *M. t. schotti* exhibited allelic differences in the *S-Aat-A* locus across their contact zone at the southern edge of the Balcones Escarpment (Fig. 11, Table 6). Both *M. t. taeniatus* and *M. t. girardi* are fixed for the *A* allele, while alleles *B* and *C* occur in *M. t. schotti* and alleles *A* and *C* are present in *M. t. ruthveni*. Neither an *M. t. girardi* (TCWC 64840), collected in Tamaulipan Biotic Province vegetation at the escarpment of the Edwards Plateau in Uvalde County, Texas, nor an *M. t. ruthveni* (TCWC 65282) from Brownsville, Texas, exhibited any protein activity at the *S-Aat-A* locus. The *A* allele was found in only one specimen of *M. t. ruthveni* from Hidalgo County, Texas, approximately 350 km south of the contact zone. The *M-Aat-A* locus also exhibited variation. The *B* allele was present at all *M. t. girardi* localities represented by more than one specimen, except the Brewster County and El Paso County, Texas, samples. This allele was also present in the homozygous state in a specimen of *M. t. taeniatus* from Socorro County, New Mexico, near the intergradation zone.

Genetic identity values were highest between *M. t. ruthveni* and both *M. t. taeniatus* and *M. t. girardi* (Table 7). The greatest genetic distances were between the parapatric *M. t. girardi* and *M. t. schotti* for all three measures used (Tables 7, 8). Even though *M. t. ruthveni* had *S-Aat-A* allele *A*, it clustered with *M. t. schotti* and not *M. t. taeniatus* or *M. t. girardi* (Fig. 12).

In addition to the results of morphological and allozyme analyses, additional evidence supporting differentiation of samples 15–17 from samples 1–14 and 22 is the absence of a broad intergradation zone between samples 14 and 15, such as the one seen in sample 22 (see systematic accounts). Only eight specimens exhibited intermediate morphological character states between samples 11–14

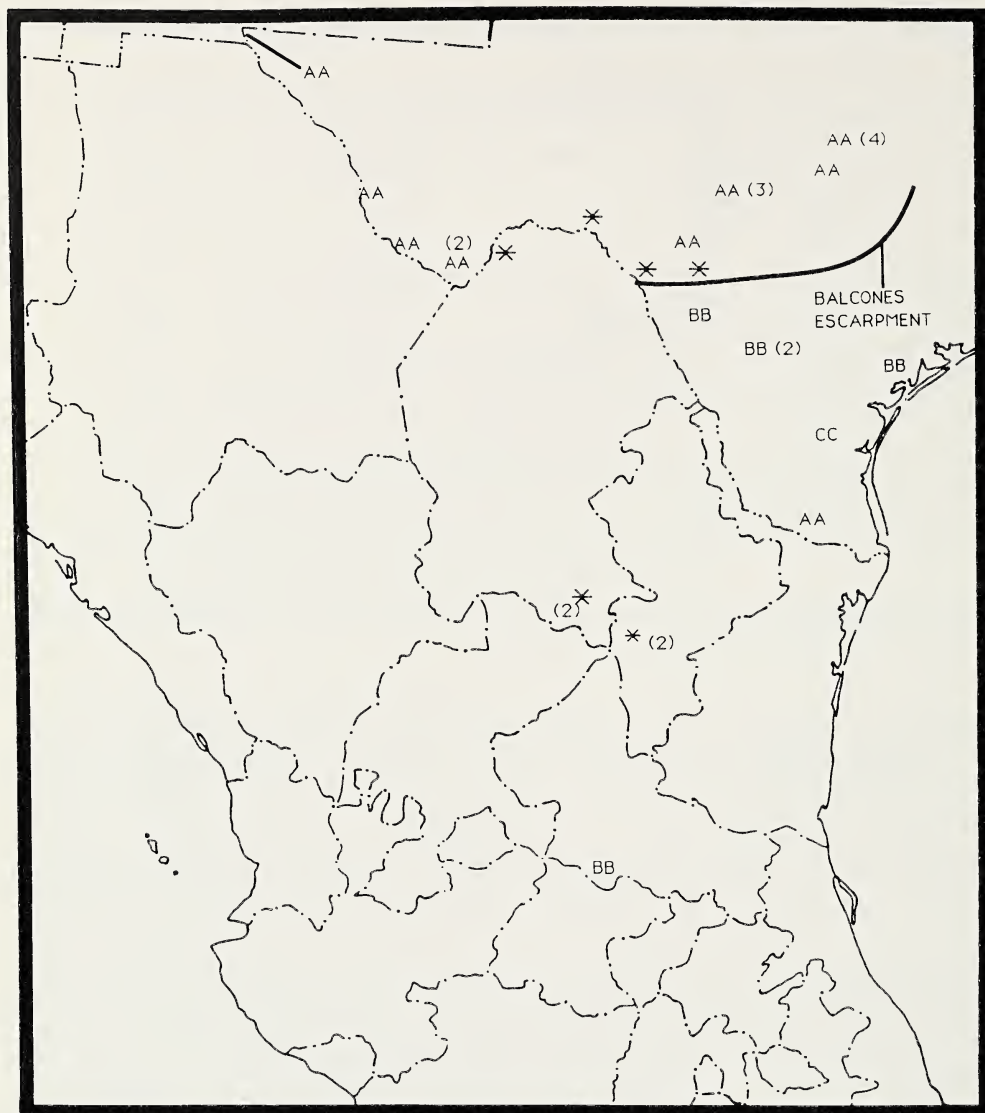


Fig. 11.—Distribution in Texas and Mexico of genotypes of the *S-Aat-A* locus and morphological hybrids. Location of hybrids denoted by an asterisk, numbers are sample sizes per locality.

and 15–17 (Fig. 11). The Balcones Escarpment contact zone between samples 14 and 15 is well-represented by specimens. Only four putative hybrids were found there (Fig. 11). Four specimens having intermediate color patterns were found at three localities in Mexico. These may represent a contact zone running northwest to southeast between samples 12 or 13 and 15 or 17 in southeastern Coahuila and western Nuevo Leon, respectively. They are considered putative hybrids, even though the nearest localities for samples 12 and 13 are in central Coahuila and central Zacatecas, respectively. This gap may be a collecting artifact. In ca-

Table 6.—*Allele frequencies at 12 polymorphic loci examined in the subspecies of Masticophis taeniatus.*

Locus and allele	<i>M. t. taeniatus</i>	<i>M. t. girardi</i>	<i>M. t. schotti</i>	<i>M. t. ruthveni</i>
<i>S-Aat-A</i>				
<i>n</i>	4	16	5	2
<i>A</i>	1.000	1.000		0.500
<i>B</i>			0.800	0.500
<i>C</i>			0.200	
<i>M-Aat-A</i>				
<i>n</i>	6	19	5	3
<i>A</i>	0.833	0.632	1.000	1.000
<i>B</i>	0.167	0.316		
<i>C</i>		0.053		
<i>Ck-A</i>				
<i>n</i>	6	16	2	3
<i>A</i>	1.000	0.937	1.000	1.000
<i>B</i>		0.062		
<i>Ck-C</i>				
<i>n</i>	6	14	2	3
<i>A</i>	1.000	0.929	1.000	1.000
<i>B</i>		0.071		
<i>Ddh-A</i>				
<i>n</i>	6	18	5	3
<i>A</i>	1.000	0.899	1.000	1.000
<i>B</i>		0.111		
<i>Est-D</i>				
<i>n</i>	6	15	5	3
<i>A</i>	1.000	0.967	1.000	1.000
<i>B</i>		0.033		
<i>Gapdh-A</i>				
<i>n</i>	5	16	5	3
<i>A</i>	0.800	0.937	1.000	1.000
<i>B</i>	0.200	0.062		
<i>S-Idh-A</i>				
<i>n</i>	6	17	5	3
<i>A</i>	1.000	0.971	1.000	1.000
<i>B</i>		0.029		
<i>Mpi-A</i>				
<i>n</i>	5	16	2	3
<i>A</i>	1.000	0.937	1.000	1.000
<i>B</i>		0.062		
<i>Pep-S</i>				
<i>n</i>	6	18	5	3
<i>A</i>	1.000	1.000	0.800	1.000
<i>B</i>			0.200	
<i>Pgm-A</i>				
<i>n</i>	6	16	3	3
<i>A</i>	1.000	0.969	1.000	1.000
<i>B</i>		0.031		
<i>Pk-A</i>				
<i>n</i>	4	14	4	2
<i>A</i>	1.000	0.964	1.000	1.000
<i>B</i>		0.036		

Table 7.—Matrix of Nei's (1972) genetic identity above the diagonal and genetic distance below, calculated from the 29 loci examined for the subspecies of *Masticophis taeniatus*.

Population	1	2	3	4
1 <i>taeniatus</i>	*****	0.997	0.967	0.989
2 <i>girardi</i>	0.003	*****	0.963	0.986
3 <i>schotti</i>	0.034	0.038	*****	0.992
4 <i>ruthveni</i>	0.011	0.014	0.008	*****

nonical discriminant analysis, the eight presumed hybrids did not have variable coefficients either similar to one another or intermediate between parental forms. Instead, Edwards Plateau hybrids grouped with either samples 1–10 or 16–17. The Nuevo Leon hybrids grouped with samples 11–14 and the Coahuila hybrids grouped with samples 1–10. These specimens show a disharmonic combination of character states typical of interspecific hybrids (Lawson and Lieb, 1990). We consider this strong evidence of severely restricted gene flow between samples 14 and 15 across the Balcones Escarpment, and of reproductive isolation of these samples. The results of phylogenetic analyses show that two monophyletic groups exist (Fig. 10), one contains samples 1–14 and 22 and the other contains samples 15–17. Therefore, samples 1–10 are considered to be *Masticophis taeniatus taeniatus* and samples 11–14 *Masticophis taeniatus girardi*, with sample 22 containing specimens intermediate between them. These appear to be reproductively isolated from sample 15, which is *Masticophis schotti schotti*, and samples 16–17, which are *Masticophis schotti ruthveni*. Samples 18–21 correspond to *Masticophis bilineatus*.

SYSTEMATICS

Masticophis taeniatus (Hallowell)

Leptophis taeniata Hallowell, 1852:181. Holotype: USNM 2110; adult male (547 mm SVL); collected by Dr. S. W. Woodhouse, date unknown. Type locality: New Mexico west of the Rio Grande; restricted to Shiprock, San Juan Co., New Mexico, USA (Smith and Taylor, 1950). See Parker (1982) for synonymies.

Definition.—A species of whipsnake with 15 anterior and midbody dorsal scale rows; four dark stripes, one in the center of each of the first four dorsal scale rows (Fig. 13); and dorsal head plates edged in cream or white (Fig. 14). Transverse light gray bands are present in some specimens (Fig. 15). All specimens lack paired light speckling on the dorsal scales and red or pink pigment immediately posterior to the angle of the jaw. Two subspecies, *M. t. taeniatus* and *M. t. girardi*, are recognized (see subspecies accounts).

Table 8.—Matrix of Rogers' (1972) genetic distance, below the diagonal, and Cavalli-Sforza and Edwards (1967) chord distance, above the diagonal, calculated from the 29 loci examined for the subspecies of *Masticophis taeniatus*.

Population	1	2	3	4
1 <i>taeniatus</i>	*****	0.090	0.190	0.117
2 <i>girardi</i>	0.026	*****	0.209	0.145
3 <i>schotti</i>	0.051	0.068	*****	0.115
4 <i>ruthveni</i>	0.030	0.046	0.022	*****

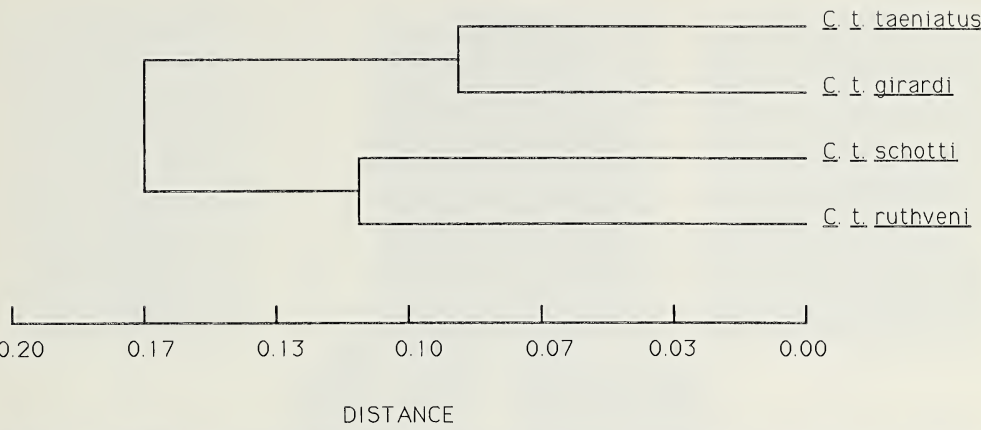


Fig. 12.—Phenogram showing the relationships of the subspecies in *Masticophis taeniatus* sensu lato, based on UPGMA of Cavalli-Sforza and Edwards (1967) chord distance from Table 14. Cophenetic correlation = 0.714.

Variation.—See Table 9 for meristic variation. Variation in primary and secondary temporal scales included 39 different arrangements in *M. taeniatus*. The lower primary temporal scale was divided, 3-2 pattern, in 531 (43.2%) specimens. No divisions, 2-2 pattern, were found in 423 (34.4%) specimens. All other temporal scale arrangements occurred at a frequency of <5%. No geographic component to temporal scale variation was found.

The number of scale row reduction sites ranged from one (15-15-13) to five (15-15-9) in both sexes of *M. taeniatus*. Most males (473, 70.9%) had three (15-

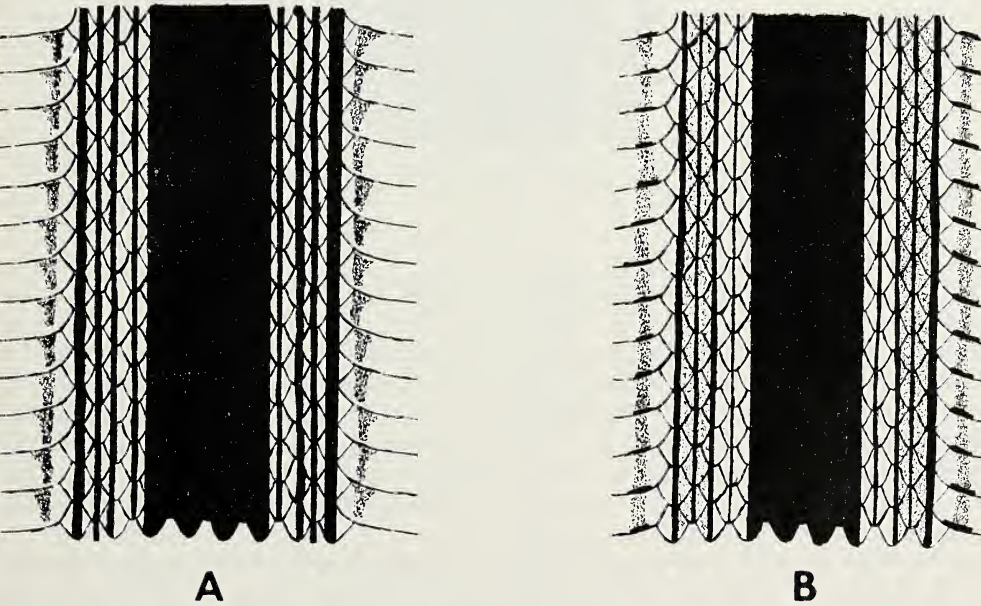


Fig. 13.—Color pattern of adult *Masticophis taeniatus taeniatus*: A) pattern found throughout subspecies' range; B) pattern found in the southern portion of its range and in smaller specimens.



Fig. 14.--Head color pattern of adult *Masticophis taeniatus taeniatus*.

15-11) reduction sites, whereas most females (446, 75.7%) have only two (15-15-12). Two reduction sites were present in 168 (25.2%) males and three reduction sites were present in 122 (20.7%) females. One reduction site (15-15-13) was present in five (0.8%) males and 17 (2.9%) females. Three (0.5%) females and 19 (2.9%) males had four reduction sites (15-15-10). Five reduction sites (15-15-9), were present in only two (0.3%) males and one (0.2%) female. Variation in SRR1 for males: \bar{x} = 121 (91-151, n = 643); females: \bar{x} = 122 (95-146, n = 576). Variation in SRR2 for males: \bar{x} = 132 (109-175, n = 633); females: \bar{x} = 139 (112-180, n = 546). Variation in SRR3 for males: \bar{x} = 159 (118-206, n = 460); females: \bar{x} = 164 (123-190, n = 119).

Distribution.—This species is found in the Great Basin and Chihuahuan deserts and the Edwards Plateau of Texas (Fig. 1). *Masticophis taeniatus* occurs north to the Snake and Columbia river valleys of Idaho and Washington, respectively. It occurs east of the Cascade Mountains, Oregon, the Sierra Nevadas, California,

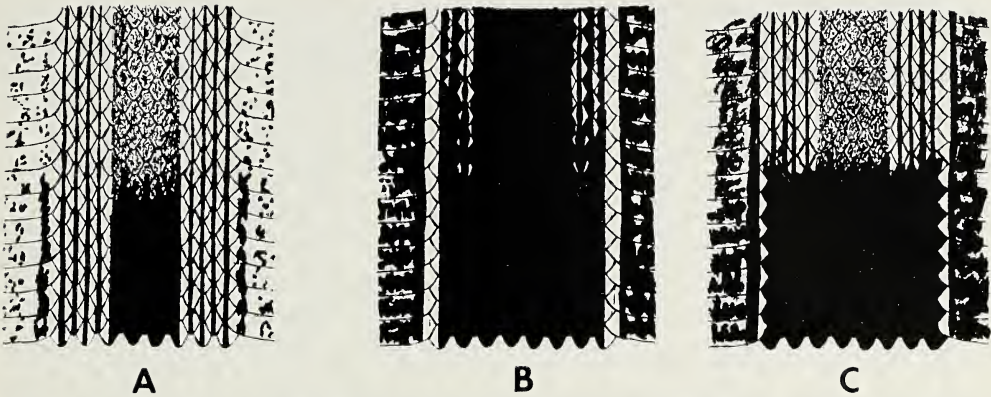


Fig. 15.—Color patterns of adult *Masticophis taeniatus girardi*: A) light pattern common throughout the Chihuahuan Desert; B) dark pattern common on the Edwards Plateau; C) intermediate pattern found throughout the subspecies' range.

and the Continental Divide in Mexico. It is absent from the Wasatch and Uinta mountain ranges in Utah. In Arizona, *M. taeniatus* is found mainly north of the Gila River. It ranges east into extreme western Colorado and to the Llano Estacado in eastern New Mexico, and south to northeastern Jalisco, Mexico. The eastern and southern range limits of *M. taeniatus* in Mexico are poorly understood.

The subspecies of *M. taeniatus* intergrade along the upper Rio Grande valley in central New Mexico (sample 22). Specimens exhibiting intermediate color patterns have been found from the vicinity of Albuquerque south to Las Cruces. This intergradation zone may be widest at the southern end, stretching from Carlsbad Caverns National Park, Eddy County, west to eastern Grant County. However, this may be an artifact of collecting because records are lacking from northern Catron, southern Valencia, and western Socorro counties in west-central New Mexico. Intergrades have a striping pattern similar to that shown in Fig. 13B, with 0–8 ($\bar{x} = 4$) faint transverse bands present anteriorly. Remnants of the nuchal collar, characteristic of *M. t. girardi* (Fig. 15), occur in most intergrades. The back, head, and stripes are usually dark gray or brown. The venter is more heavily pigmented than in most *M. t. taeniatus*, but less so than in *M. t. girardi*. Thirty-seven male and 31 female intergrades were examined.

Masticophis taeniatus taeniatus (Hallowell)
(Fig. 13, 14)

Definition and Diagnosis.—The desert striped whipsnake, *M. t. taeniatus*, has 15 dorsal scale rows anteriorly and at midbody, light borders on head scales, and four dark longitudinal stripes. It is the only *Masticophis* with 15 dorsal scale rows lacking transverse bands, dark ventral mottling, light dorsal speckling, and red pigment at the angle of the jaw. *Masticophis t. taeniatus* has fewer subcaudals and maxillary teeth than *M. t. girardi*.

Distribution.—*Masticophis t. taeniatus* has primarily a Great Basin Desert distribution (Fig. 1). It occurs south into southwestern New Mexico east of the Continental Divide. Its range slightly overlaps the range of *M. bilineatus* across central and southeastern Arizona. *Masticophis t. taeniatus* does not occur in Mexico or Texas, contrary to what Ortenburger (1928), Parker (1982), and Conant

Table 9.—*Meristic variation among Masticophis taeniatus, M. schotti, and M. bilineatus. An asterisk indicates a modal value for that character and a plus sign indicates that supralabials 4 and 5 contact the eye.*

Characters		<i>M. taeniatus</i>			<i>M. schotti</i>			<i>M. bilineatus</i>		
		\bar{x} (SD)	Range	n	\bar{x} (SD)	Range	n	\bar{x} (SD)	Range	n
Ventral	M	204 (7.0)	183-236	647	195 (5.8)	181-212	170	200 (6.9)	182-221	163
	F	205 (6.3)	187-232	575	198 (6.6)	181-218	120	199 (6.3)	183-216	157
SC	M	144 (10.6)	117-175	472	145 (9.1)	120-166	106	141 (9.1)	120-167	79
	F	138 (10.8)	105-178	393	139 (9.6)	113-162	77	137 (8.7)	121-165	73
Maxillary teeth		18.3 (1.2)	15-23	1196	17.5 (1.0)	15-21	268	19.3 (0.8)	17-23	300
Hemipenis length (SC)		8.7 (1.8)	4-15	420	8.8 (1.5)	6-13	81	8.0 (1.6)	5-14	103
Supralabials +		8*	7-9	1229	8*	6-9	290	8*	7-9	321
Infralabials		9*	8-11	1229	9*	8-10	289	9*	8-11	321
Preoculars		2*	1-3	1229	2*	1-3	289	2*	none	321
Postoculars		2*	1-3	1229	2*	1-3	289	2*	2-4	321
Loreals		1*	1-2	1251	1*	1-3	305	1*	1-2	309
Scale pits		2*	0-3	1229	1*	0-3	289	1*	0-2	321

and Collins (1991), report. Only two specimens from Washington were examined (Appendix 1) and additional localities (Nussbaum et al., 1983) for Washington were not confirmed. The specimen from near Oakland, Alameda County, California (CAS 10639) is a *M. t. taeniatus*, but we believe its locality data are incorrect.

Color Pattern Variation.—This subspecies shows little variation in color pattern. The head, back, and stripes are usually dark olive green, but may be brown to almost black in some southern specimens. In many smaller, presumably younger specimens and those from the southern part of its range, lateral stripes 2 and 4 are lighter than stripes 1 and 3, with a slight darkening between stripes 1 and 3 (Fig. 13B), but the pattern depicted in Fig. 13A is most common. The head plates are edged with light pigment (Fig. 14). In life, the posterior quarter of the venter and entire ventral surface of the tail are pink. The rest of the venter is usually cream with a blurry stripe on the lateral portions of the ventrals (Fig. 13). More than 90% of each sample has black spotting on the lower jaw, throat, and neck regions (Fig. 3). Northern specimens have dark ventral pigment occurring at high frequencies; samples 1–3 (32%–46%). Dark ventral pigmentation occurs at frequencies of <15% in all other samples except sample 9 (39% with dark ventral pigment). This may be due to the influence of *M. t. girardi*.

Masticophis taeniatus girardi (Stejneger and Barbour)
(Fig. 15, 16)

Masticophis ornatus Baird and Girard, 1853:102. Holotype: USNM 1971; skin of adult, sex unknown, collected by J. D. Graham, date unknown. Type locality: USA, Texas, between San Antonio and El Paso; restricted to Fort Davis, Jeff Davis Co. (Smith and Taylor, 1950). See Parker (1982) for synonymies.

Coluber taeniatus girardi Stejneger and Barbour, 1917:89.

Diagnosis.—The central Texas whipsnake, *M. t. girardi*, differs from *M. t. taeniatus* in having transverse light banding, darker dorsal and ventral coloration, and higher subcaudal and maxillary tooth counts. It lacks the dorsal light flecking and red pigment at the angle of the jaw that are present in *M. schotti*.

Distribution.—*Masticophis t. girardi* has a Chihuahuan Desert–western Mexican Plateau distribution with an eastward extension onto the Edwards Plateau of Texas (Fig. 1). The hiatus in the range of *M. t. girardi* in southern Coahuila, northern Zacatecas, and northwestern San Luis Potosi, Mexico, may be a sampling artifact. The western boundary of the range follows the continental divide with a few localities west of it in Durango and northeastern Jalisco, Mexico. In central Texas, the range limits of *M. t. girardi* closely follow the Balcones Escarpment. A Throckmorton County, Texas, specimen (TNHC 26579) is typical *M. t. girardi*, but is so far out of range that its locality data are believed to be incorrect (Dixon, 1987).

Color Pattern Variation.—The dorsal head plates are light edged in all but the darkest specimens (Fig. 16). A light collar is present in all specimens, but is broken into two light nape blotches by dark pigment in 48.9% of specimens examined (Fig. 16). The lateral portions of the collar (nape blotches) range from one to five scales wide. Most specimens (42.3%) have nape blotches three scales wide, whereas 40.9% have them two scales wide. The medial collar width ranges up to five scales, with 48.9%, 23.3%, 14.0%, and 10.7% having a medial collar width of zero, one, two, and three scales wide, respectively. Dorsal light bands, posterior to the collar, range from zero to ten, averaging 5.3 in 479 specimens. No geographic variation in band number was found.



Fig. 16.—Head color pattern of adult *Masticophis taeniatus girardi*.

The dorsal color patterns illustrated in Fig. 15 represent the ends of a continuum of variation. Fig. 15C represents a common intermediate condition. Pattern 15A differs from 15C in that some light areas are present between stripes, especially stripes 3 and 4. Color patterns were scored as belonging to one of these three

Table 10.—Dorsal color pattern frequencies found among samples 11–14 of *Masticophis taeniatus girardi* shown in Fig. 3. Pattern types refer to Fig. 15.

Sample	Pattern		
	Light (15A)	Dark (15B)	Intermediate (15C)
11	64.70%	16.81%	18.48%
12	81.08%	2.70%	5.41%
13	88.00%	4.00%	8.00%
14	13.70%	60.27%	15.34%

patterns (Fig. 15). The light pattern (Fig. 15A) is more common throughout the Chihuahuan Desert (samples 11–13, Table 10). The dark pattern (Fig. 15B) is dominant on the Edwards Plateau (sample 14), occurring at low frequencies in samples 11–13. Specimens scored as intermediates (Fig. 15C) were most common in the northern part of the range (samples 11 and 14) and occur at low frequencies in samples 12–13 (Table 10). The anterior ventral pattern of *M. t. girardi* consists of black pigment covering >50% of the chin shields, gulars, and anterior ventrals in >99% of specimens. The belly is mostly black in >92% of specimens. The subcaudals have dark pigment confined to the lateral edges in >88% in samples 11–14 (Fig. 3). The posterior quarter of the venter and the subcaudals are pink in life. In dark specimens, the pink may be reduced to only the small areas between the dark blotches on the ventrals.

The predominance of the dark pattern (Fig. 15B) on the Edwards Plateau may be associated with thicker vegetation such as *Juniperus*. Five melanistic specimens of *M. t. girardi* were found. One such Edwards Plateau specimen is an adult female 1090 mm SVL (CAS 103476) from Val Verde County, Texas. Three additional specimens (CM 48192, LACM 116256, and KU 80828) are from the Cuatro Ciénegas basin in central Coahuila, Mexico (Camper and Dixon, 1990). Another specimen (KU 39567) is an adult female (938 mm SVL) from western Coahuila, Mexico.

Masticophis schotti (Baird and Girard)

Masticophis schotti Baird and Girard, 1853:160. Holotype: USNM 1972, adult male (943 mm SVL) collected by Arthur Schott, date unknown. Type locality: Eagle Pass, Maverick Co., Texas, USA. See Parker (1982) for synonymies.

Definition.—The only species of *Masticophis* with 15 anterior and midbody dorsal scale rows, paired white, cream, or yellow spots on the anterior corners of the dorsal scales, uniformly dark head plates, and red pigment immediately posterior to the jaw angle. Two subspecies, *M. s. schotti* and *M. s. ruthveni*, differ from one another primarily in color pattern. See subspecies accounts for descriptions of type specimens and color patterns.

Variation.—See Table 9 for meristic variation. Thirty-one temporal scale patterns were found. The nondivided 2-2 pattern was the most frequent, 35.3% (102 specimens). The lower primary was divided, 3-2 pattern, in 69 (23.9%) specimens. The lower primary and secondary temporals were fused in 33 (11.4%) specimens. Other temporal scale arrangements existed at frequencies <5% with no geographic variation discernible.

The number of scale row reduction sites ranged from one (15-15-13) to four (15-15-10) in males and from one to three (15-15-11) in females. Most males (96, 54.9%) had two (15-15-12) reduction sites, whereas most females (97, 74.1%) had only one (15-15-13). Two reduction sites were present in 30 (22.9%) females and one reduction site was present in 24 (13.7%) males. Three reduction sites (15-15-11) were present in 53 (30.3%) males and four (3.1%) females. Two (1.1%) males had four reduction sites (15-15-10). Variation in SRR1 in males: \bar{x} = 119 (88–139, n = 165); females: \bar{x} = 117 (76–138, n = 118). Variation in SRR2 in males: \bar{x} = 151 (112–184, n = 137); females: \bar{x} = 157 (115–186, n = 30). Variation in SRR3 in males: \bar{x} = 159 (136–190, n = 49); females: \bar{x} = 161 (154–172, n = 4).

Distribution.—This species is found from the Balcones Escarpment of central Texas south to the Gulf Coastal Plain and inland onto the Mexican Plateau (Fig. 1). The western limits of its range in northern Mexico are unclear.

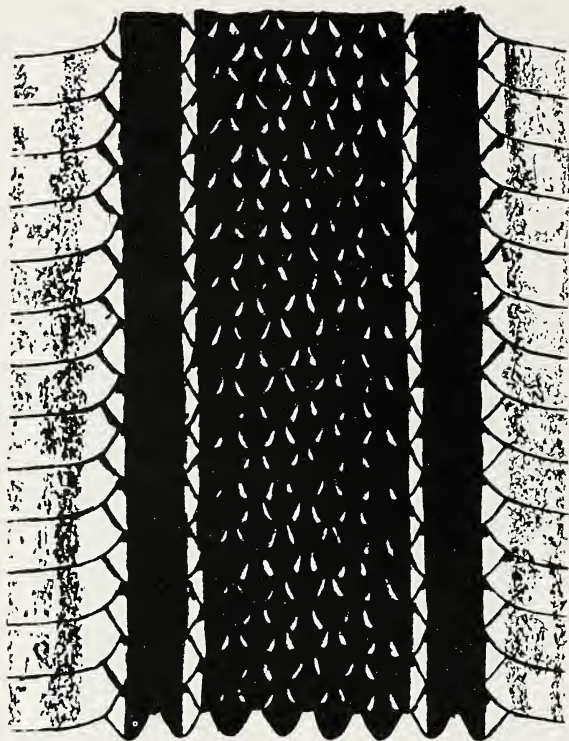


Fig. 17.—Color pattern of adult *Masticophis schotti schotti*.

Masticophis schotti schotti (Baird and Girard),
new combination
(Fig. 17, 18)

Definition and Diagnosis.—*Masticophis s. schotti* has 15 anterior and midbody dorsal scale rows, paired cream-colored light spots on the anterior dorsal scale corners and invariably two prominent light stripes. It differs from *M. s. ruthveni* in having lighter ground color, lighter dorsal speckling, and a more prominent upper light stripe that always extends past ventral 110.

Distribution.—The geographic range of *M. s. schotti* is apparently restricted to the Tamaulipan Biotic Province of Blair (1949; Fig. 1). Few specimens from Mexico exist, and the western range limits in the Coahuila Folded Belt Region are unclear.

Color Pattern Variation.—Adult *M. s. schotti* are invariant in color pattern (Fig. 17). The grayish-green ground color does not fade in preservative. In life, the subcaudals are pink in most specimens, except for their lateral tips which are grayish-green. Grayish-green speckling is present on the subcaudals in 15.0% of *M. s. schotti* examined. The red pigment behind the jaw angle fades in preservative.

Masticophis schotti ruthveni (Ortenburger),
new combination
(Fig. 18, 19)

Masticophis ruthveni Ortenburger, 1923:2. Holotype: UMMZ 57681, adult male (1104 mm SVL), collected by A. I. Ortenburger, date unknown. Type locality: Brownsville, Cameron Co., Texas, USA. Paratypes: UMMZ 57682–57684 and 57686–57694, UIMNH 43493, and MCZ 62561.



Fig. 18.—Head color pattern of adult *Masticophis schotti* and *Masticophis bilineatus*.

Masticophis taeniatus australis Smith, 1941:390. Holotype: USNM 10240, juvenile female, collected by A. Duges in 1879. Type locality: "Guanajuato," Guanajuato, Mexico. New synonymy.

Definition and Diagnosis.—Ruthven's whipsnake, *M. s. ruthveni*, has 15 anterior and midbody dorsal scale rows, paired dorsal spotting, and a variable color pattern. Because the holotype of *M. t. australis* is a typical juvenile *M. s. ruthveni*, we herein synonymize the former. It differs from *M. s. schotti* in having narrower, fainter stripes that are variable in number, darker dorsal spots, and a more variable ground color that is usually darker. The upper light stripe does not extend to ventral 110.

Distribution.—*Masticophis s. ruthveni* is found on the Gulf Coastal Plain from the Rio Grand south to central Veracruz, Mexico (Fig. 1). Gaps along the east coast of Mexico in Tamaulipas and Veracruz are believed to result from collecting bias. This taxon ranges west into the Sierra Madre Oriental and onto the southern part of the Mexican Plateau west to northern Michoacan. The western range limits of *M. s. ruthveni* are unclear. Two putative *M. t. girardi* × *M. s. ruthveni* hybrids

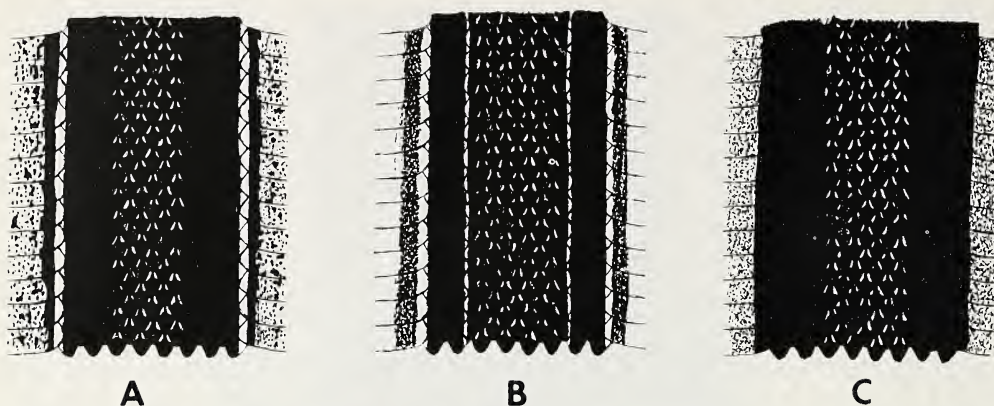


Fig. 19.—Color patterns of adult *Masticophis schotti ruthveni*: A) two-striped pattern most common throughout the subspecies' range; B) four-striped pattern found uncommonly throughout the subspecies' range; C) rare stripeless pattern.

from central Nuevo León indicate that *M. s. ruthveni* may not occur as far west in northern Mexico as it does on the southern part of the Mexican Plateau. In the USA, this subspecies occurs in Cameron, Hidalgo, Starr, Willacy, and south central Kenedy counties, Texas. The juvenile identified as *M. s. schotti* by Martin (1958) from La Joya de Salas, Tamaulipas, Mexico, (UMMZ 110818) is a *M. s. ruthveni*, as is UIMNH 3836 from 25 miles south of Monterrey, Nuevo León, Mexico (Shannon and Smith, 1949).

Color Pattern Variation.—Specimens exhibiting only the lower light stripe were the most common, occurring at a frequency of 56.8% (Fig. 19A; Table 11). Two light stripes were found in 37.5% of *M. s. ruthveni* (Fig. 19B). The upper light stripe, occurring on the upper margin of scale row 3 and lower margin of scale row 4, is narrow and faint. It extended as far posterior as ventral 110 (*M. s. schotti* character state) in only four (3.5%) *M. s. ruthveni*. The 5.8% of *M. s. ruthveni* that lacked stripes had a dark olive, almost black, ground color with bright yellow dorsal speckling (Fig. 19C). Stripeless specimens occur in southern Tamaulipas and eastern and southwestern San Luis Potosi, Mexico. Little geographic variation in color pattern was found. The frequencies of the one- and two-striped morphs are equal in the lowland sample 16 (Table 11). The ventral color pattern varies from dense speckling on the lateral quarter of the ventrals to sparse speckling toward the ventral midline, except in stripeless specimens, where dense ventral speckling is present throughout. The venter is the same color as the dorsum in striped specimens. In stripeless specimens, it is lighter toward the midline. Dorsal

Table 11.—Dorsal color pattern frequencies found among samples 16–17 *Masticophis schotti ruthveni* shown in Fig. 3. Pattern types refer to Fig. 19.

Pattern	Sample	
	16	17
1-stripe (19A)	42.86%	67.80%
2-stripes (19B)	42.86%	22.03%
0-stripes (19C)	14.29%	10.17%

pigment extends ventrally to the lateral subcaudal tips. Medially, the subcaudals are pink in living specimens.

Masticophis bilineatus Jan
(Fig. 18, 20)

Masticophis bilineatus Jan, 1863:65. Holotype: MTKD 15523, female (467 mm SVL), date of collection and collector unknown. Type locality: Restricted to Guaymas, Sonora, Mexico (Smith and Taylor, 1950). Restriction of type locality to Casas Grandes, Chihuahua by Schmidt (1953) is in error (see remarks).

Bascanium semilineatum Cope, 1891:626. Holotype: USNM 1981, female, 816 mm SVL, collected by A. Schott, date unknown. Type locality: Colorado River bottom, Arizona.

Zamenis semilineatus: Gunther, 1894:121.

Bascanion semilineatum: Van Denburgh, 1896:347.

Coluber semilineatus: Stejneger and Barbour, 1917:80.

Masticophis semilineatus: Ortenburger, 1923:2.

Coluber bilineatus: Bogert and Oliver, 1945:362.

Masticophis bilineatus lineolatus Hensley, 1950:272. Holotype: UIMNH 5611, male, 1011 mm SVL, collected by M. Hensley, 23 May 1949. Type locality: North branch of Alamo Canyon, Ajo Mountains, 12.9 mi S and 5 mi E of the Ajo-Tucson-Sonoyta junction, Pima Co., Arizona. New synonymy.

Masticophis bilineatus slevini Lowe and Norris, 1955:93. Holotype: SDNHM 3826, female, 833 mm SVL, collected by Mrs. G. Bancroft, 18 April 1930. Type locality: Isla San Esteban, Gulf of California, Sonora, Mexico. New synonymy.

Definition and Diagnosis.—*Masticophis bilineatus* is the only striped *Masticophis* with a combination of 17 anterior and midbody dorsal scale rows, two dark lateral stripes on each side of the body, and paired light spots on the anterior corners of the dorsal scales. Because the previously described subspecies do not differ from other populations in the characters on which their descriptions were based, we herein synonymize them with *M. bilineatus*. It differs from *M. taeniatus* and *M. schotti* in having more dorsal scale rows. It differs from other striped whipsnakes that have 17 dorsal scale rows in dorsal ground color and by possessing paired light spots on the dorsal scales.

Description of Holotype.—Dorsal scale rows 17-17-13. A portion of the venter is missing and the tail is incomplete so ventral and subcaudal counts were not made. A paratype, (MTKD 15068) an adult female (748 mm SVL) has 196 ventrals, 130 subcaudals and 17-17-13 dorsal scale rows. The paratype has a dorsal scale row reduction formula as follows:

$$17 \frac{3 + 4(114)}{3 + 4(114)} 15 \frac{7 + 8(118)}{7 + 8(118)} 14 \frac{6 + 7(124)}{6 + 7(124)} 13(196)$$

Scale row reduction sites of the holotype involve the same dorsal scale rows as those of the paratype. The holotype has 20 maxillary teeth and one apical scale pit. It has a divided anal plate; supralabials 8-9; infralabials 11-10; preoculars 2-2; postoculars 2-2; and loreals 1-1. Supralabials 4 and 5 contact the right orbit and supralabials 5 and 6 contact the left orbit. Supralabial 3 on the left side is divided. Both right primary temporals are divided, 4-2 pattern, and all but the lower left secondary are split, 4-3 pattern.

The color pattern is characteristic for the species (Fig. 20B). Two dark stripes are present, the lower stripe is located on the lower half of scale row 1 and adjacent tips of the ventrals, and the upper stripe is located on the upper half of scale row 2 and lower half of scale row 3. The dorsal scales have paired light spots at their anterior corners. The dorsal coloration is dark olive green fading to light green

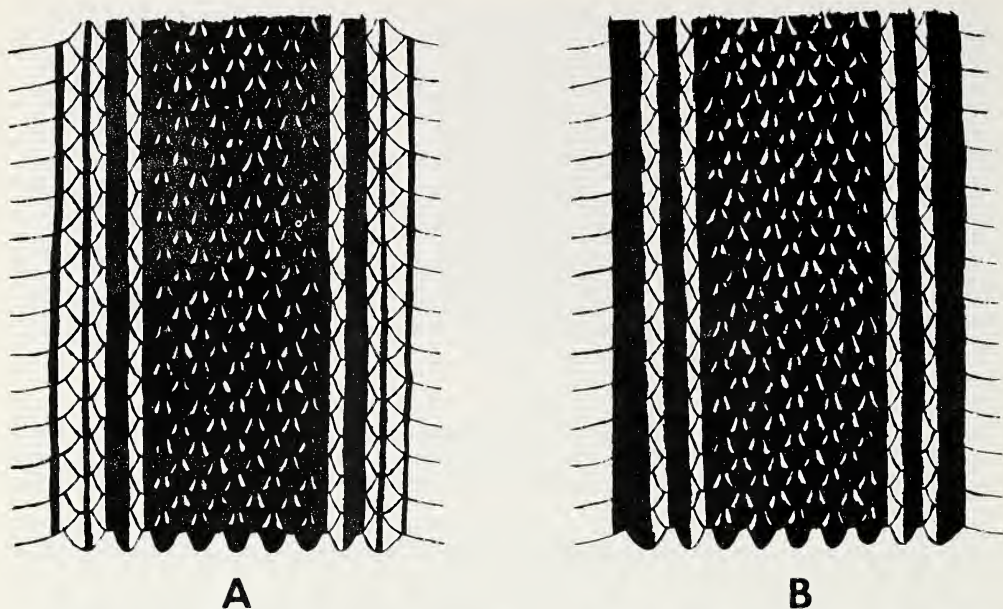


Fig. 20.—Color pattern of adult *Masticophis bilineatus*: A) lighter pattern more common in larger specimens; B) darker pattern more common in smaller specimens.

posteriorly. The light stripe between the upper dark stripe and the middorsum does not fade anterior to ventral 110. The head plates are uniformly colored the same shade as the dorsum (Fig. 18). The venter is immaculate except for the dark spots present on the chin shields, gulars, and first 10–15 ventrals. The subcaudals are also immaculate, except for their lateral tips, which are the same color as the dorsum.

Remarks.—We believe that Schmidt (1953) is in error in restricting the type locality of *M. bilineatus* to Casas Grandes, Chihuahua, Mexico. This locality is east of the continental divide where this species does not occur.

Variation.—See Table 9 for meristic variation. Thirty-one right temporal scale patterns were recorded for *M. bilineatus*. A divided lower primary, 3-2 pattern, occurred in 72 (22.4%), 64 (19.9%) had all but the lower secondary divided, 4-3 pattern. No temporals were divided in 52 (16.2%), both primary temporals were divided, 4-3 pattern, in 30 (9.4%). Other temporal scale patterns occurred at frequencies <5%. No geographic component to temporal scale variation was found.

The number of scale row reduction sites ranged from two to five in males and from two to six in females. Most males (150, 91.5%) and females (155, 95.1%) had three reduction sites (17-17-13). Eleven (6.7%) males and five (3.1%) females had four (17-17-12) scale row reduction sites. One (0.6%) male and two (1.2%) females had only two (17-17-14) reduction sites. Two (1.2%) males had five (17-17-11) reduction sites and one (0.6%) female had six (17-17-10) reduction sites. Variation in SRR1 for males: \bar{x} = 115 (81–136, n = 158); females: \bar{x} = 114 (91–129, n = 153). Variation in SRR2 in males: \bar{x} = 123 (91–167, n = 154); females: \bar{x} = 121 (93–154, n = 147). Variation in SRR3 in males: \bar{x} = 130 (108–192, n = 117); females: \bar{x} = 127 (95–189, n = 121).

Distribution.—In the north, *M. bilineatus* has a Sonoran Desert distribution that interdigitates with that of *M. t. taeniatus* in eastern and central Arizona. Sympatric populations may occur in southwestern Yavapai County, western Gila County, and southern Graham County, Arizona. *Masticophis bilineatus* and *M. t. girardi* appear to be parapatric in western Durango and northern Jalisco, Mexico. In New Mexico, USA, and northern Sonora, southern Zacatecas, northern Jalisco, and Aguascalientes, Mexico, the eastern range limits of *M. bilineatus* follow the Continental Divide. From the Sonoran Desert it occurs south along the Gulf of California lowlands to Colima with an eastward range extension onto the Mexican Plateau in Jalisco, Aguascalientes, and Zacatecas. The specimen supposedly from Isla San Pedro Martir (UO 32528) is probably from Isla San Esteban (D. Hews, personal communication). Two specimens, both labelled MCZ 4582, from San Pedro, Coahuila, Mexico, are *M. taeniatus* and *M. bilineatus*. Since the latter is so far out of range, the locality data are believed to be incorrect. The same is true for USNM 46499, purportedly from Cuicatlam, Oaxaca, Mexico.

Color Pattern Variation.—The dorsal color pattern of *M. bilineatus* varies little, with both patterns present in specimens of all sizes and from all of its range (Fig. 20). The head plates of *M. bilineatus* are uniformly dark and identical in shade to the rest of the dorsum (Fig. 18). Pattern 20B is most common in smaller individuals, whereas pattern 20A is more common in larger specimens. An adult male (TCWC 21903, 733 mm SVL) from Mazatlán, Sinaloa, Mexico, has an aberrant color pattern. The light line between the upper dark stripe and the back is absent, forming a uniformly dark dorsum starting at the upper half of scale row 2 on each side. Dark pigment is present on the lateral tips of the ventrals and on the ventral and posterior edges of each scale in row 1, forming a narrow diffuse lower dark stripe. The paired cream-colored spots at the anterior corners of the dorsal scales are present in this and all adult *M. bilineatus*.

The ventral color pattern of *M. bilineatus* varies little, with dark spotting present on the chin shields, gulars, and first 10–15 ventrals in 131 (45.6%) specimens, and absent in 168 (54.4%). Ventral spots form a median row that usually extends 10–15 ventrals posterior to the head, but in the Isla San Esteban population it extends approximately 40 ventrals farther posteriorly. Dark spotting on the belly was present in only 37 (12.0%) specimens, whereas 272 (88.0%) lacked belly spotting. Dark spotting was present on the subcaudals of 137 (44.3%) *M. bilineatus*, 175 (55.7%) had dark pigment on the lateral subcaudal tips only. Subcaudal spotting occurred at a frequency of about 50% in samples 18 and 19, but was virtually absent from samples 20 and 21 (Fig. 3).

DISCUSSION

Masticophis taeniatus and *M. schotti* are well-differentiated morphologically. Many color pattern differences are obvious and were weighted highest by the canonical discriminant analysis (see species accounts). Additionally, *M. taeniatus* and *M. schotti* differ in a number of meristic and mensural character states. The differences are greatest between *M. t. girardi* and *M. s. schotti* across the southern Balcones Escarpment. They differ in *M. t. girardi* having a higher frequency of three SRR sites, two apical scale pits, higher maxillary tooth counts, significantly higher mean ventral counts, and significantly smaller mean HWSVL. The Balcones Escarpment is a well-known geographic boundary for many reptile species, including 37 species of snakes (Smith and Buechner, 1947). The occurrence of *M.*

t. girardi (TCWC 64840) off the Edwards Plateau in Tamaulipan desert vegetation establishes the existence of a narrow zone of sympatry between *M. t. girardi* and *M. s. schotti*. The locality is about 38 km southwest of the nearest *M. t. girardi* locality and approximately 33 km northwest of the nearest *M. s. schotti* locality. A hybrid specimen (TCWC 49204) is known from a locality 20 km to the east. Increases in ventral counts in *M. s. ruthveni* and decreases in maxillary tooth and ventral counts of *M. t. taeniatus* away from the contact zone may indicate character displacement (Mayr, 1970). Discordant patterns of character state distributions are found in intermediate specimens from this area, indicating that they may be interspecific hybrids (Lawson and Lieb, 1990). Evidence suggests that the southern Balcones Escarpment may be a narrow hybrid zone (sensu Moore, 1977).

Two additional contact zones may exist between *M. taeniatus* and *M. schotti*. The first of these is the previously mentioned area of northeastern Mexico, where four putative hybrids were found. However, this is problematical, because no specimens of *M. t. girardi* are known as yet from near this locality. The second is a *M. t. girardi* (CAS 165260) from northeastern Jalisco which is sandwiched in an area of parapatry between the ranges of *M. s. ruthveni* and *M. bilineatus*, suggesting a potential contact zone involving all three species.

Despite character state similarities among these three species, and areas of sympatry involving *M. taeniatus* and *M. bilineatus*, no hybrids involving the latter species were found. *Masticophis bilineatus* differs from the other two species in having the plesiomorphic character state of 17 dorsal scale rows. *Masticophis taeniatus* and *M. schotti* are shown to be sister species on the basis of the synapomorphic condition of 15 dorsal scale rows. Little intraspecific variation in anterior and midbody dorsal scale rows are known for any *Masticophis*. Thus, *M. bilineatus* is considered the most divergent of the three species examined.

Southward decreases in ventrals of *M. bilineatus* (Fig. 4, 5) as found in this study were also reported by Ortenburger (1928). Ventral variation among samples 18–21 indicates a step cline, whereas subcaudal variation is more gradual (Fig. 4–7). Differences between snake populations inhabiting Sonora and Sinaloa were discussed for *M. flagellum* (Wilson, 1970) and *Hypsiglena* (Dixon and Dean, 1986). The latter authors identified a hybrid zone in the foothills along the Río Fuerte in northern Sinaloa that is a transition area from lower Sonoran Desert vegetation to tropical thorn scrub. Two male *M. bilineatus* from the lowlands along the Río Fuerte agree with northern (Sonoran Desert) specimens in ventral number. Perhaps the contact zone between the low and high ventral count forms is farther east in the foothills, as in *Hypsiglena*, or immediately to the south of the Río Fuerte. However, no specimens of *M. bilineatus* and *Hypsiglena* are available from between Los Mochis and Guamuchil, Sinaloa (Dixon and Dean, 1986). The southern low-ventral form of *M. bilineatus* may constitute a separate subspecies (C. H. Lowe, personal communication). However, multivariate analyses did not separate these samples (Fig. 8, 9) and *Masticophis bilineatus* is therefore considered monotypic.

Genetic differentiation is low among the taxa examined here. Since other snake species are known to show low levels of genic differentiation (Gartside et al., 1977; Murphy and Ottley, 1980; Murphy, 1983; Murphy and Crabtree, 1985; Lawson, 1987; Lawson and Lieb, 1990), this is not indicative of measurable gene flow. Murphy (1983) reported Nei's genetic identity values of 0.89 between *Masticophis lateralis* and *M. aurigulus*, and 0.94 between *Crotalus ruber* and *C. catalinensis*. Speciation with little genic differentiation is well-known among many taxa (see

citations in Gartside et al., 1977). They reported Rogers' *S* values of 0.91–0.94 with little morphological differentiation between the ribbon snakes, *Thamnophis proximus* and *T. sauritus*. Rogers' *S* values among the morphologically better-differentiated *M. taeniatus* and *M. schotti* range from 0.93–0.97. Degree of genic differentiation is more closely associated with time since divergence (Avise and Ayala, 1976). Differentiation of *M. schotti* and *M. taeniatus* may have resulted from a Recent speciation event, possibly divergence in allopatry during habitat changes brought about by Wisconsin glaciation, with secondary contact occurring presently along the Balcones Escarpment. Populations of whipsnakes now known as *M. taeniatus* may have been isolated in the Chihuahuan Desert refugia of north-central Mexico, while the ancestors of *M. schotti* were restricted to the Tamaulipan grassland refugium of eastern Mexico (Morafka, 1977). However, because *M. taeniatus* and *M. schotti* are sister species, one cannot distinguish between a primary and secondary origin for the Balcones Escarpment contact zone (Wiley, 1981).

The existence of the *A* allele of the *S-Aat-A* locus in one specimen of *M. s. ruthveni* from extreme southern Texas is problematical. Three possibilities exist. First, the presence of this allele in *M. schotti* may be the result of introgression from *M. t. girardi* in Mexico. This may occur at one of the two potential contact zones previously mentioned. With the apparent absence of *M. t. girardi* near the potential contact zone in northern Mexico, and a lack of intermediate specimens from the south-central Mexican plateau area, little evidence in support of this hypothesis exists. Second, the observed pattern of geographic variation in alleles at this locus may be a function of small sample size, with all alleles being present in both species. It has been shown that sample sizes as small as those used here are adequate for estimating genetic divergence (Nei, 1978; Gorman and Renzi, 1979). However, answering this question necessitates a population genetics approach and not simply a measure of genetic divergence. Even though sample sizes are insufficient for population genetic studies of these species, the fixed difference across the Balcones Escarpment contact zone appears real. Evidence for this hypothesis lies in the step clinal pattern of variation of several morphological characters and the paucity of specimens with intermediate phenotypes or genotypes. Finally, the *A* allele of the *S-Aat-A* locus may be a residual allele common to the ancestor of *M. schotti* and *M. taeniatus* such as that hypothesized for *Anguilla* by Avise et al. (1990). It appears that there is character state divergence at the *S-Aat-A* locus with respect to the Balcones Escarpment contact zone, with the *A* allele not yet extinct in *M. schotti* populations located away from the contact zone. Since *M. schotti* is variable at this locus, with the *A* allele still present, Recent divergence with differential selection pressures within each of these two species is suspected. The last hypothesis is preferred, since it is most concordant with the more conclusive morphological data set. However, more specimens from throughout the ranges of both species must be assayed for genetic variation in order to fully test these hypotheses.

Although we have not previously discussed the relationship of *Masticophis* to other related genera, for example *Coluber*, *Mastigodryas*, *Dendrophidion*, and possibly *Drymobius*, at this time we do not propose the synonymy of *Masticophis* and *Coluber*. It is obvious to us that the latter genera may well be congeneric, as suggested by Schätti (1986, 1987) and Stejneger and Barbour (1917). We suspect that *Masticophis* sensu stricto is not a valid genus because of the evidence from osteology and hemipenis morphology presented by Schätti (1986, 1987).

ACKNOWLEDGMENTS

We would like to thank the following for live specimens or tissue samples: R. Baker, B. Buchanan, J. Campbell, L. Densmore, C. Farquhar, R. Green, C. Harrison, R. Jennings, J. Johnson, B. Keeley, K. King, W. Lamar, T. Lee, C. Lieb, R. Macken, R. Martin, H. McCrystal, P. Mckeown, A. Price, A. Rentfro, N. Scott, R. Wallace, R. Worthington, and the Texas Herpetological Society. Special thanks go to R. and B. Houston, who graciously gave us access to their land in Llano County, Texas. Marc Allard, G. Baumgardner, H. Camper, J. Derr, I. Greenbaum, H. Greene, B. Hanks, M. Morris, A. Price, M. Retzer, K. Reed, M. Sims, S. Smith, and P. Sudman provided help during data collection or analysis. We thank the following institutions (and curators) for loans of specimens: American Museum of Natural History (AMNH, C. Myers, R. Zweifel), Academy of Natural Sciences, Philadelphia (ANSP, J. Cadle, E. Malnate), Angelo State University (ASC, M. Engstrom), Arizona State University (ASU, M. Douglas), Baylor University–Strecker Museum (SM, D. Lintz), Brigham Young University (BYU, J. Sites), Chicago Academy of Sciences (CA, R. Vasile), California Academy of Sciences (CAS, R. Drewes, J. Vindum), Carnegie Museum of Natural History, Pittsburgh (CM, E. Censky, C. J. McCoy), Cornell University (CU, K. Adler, R. Schoknecht), Dallas Museum of Natural History (DMNH, K. Krumke), Drake University (DURC, J. Christiansen), Ernest A. Liner (EAL), Field Museum of Natural History, Chicago (FMNH, H. Marx), Fort Worth Museum of Science and History (FWM, W. Voss), Illinois Natural History Survey (INHS, K. Cummings, L. Page, M. Retzer), University of Kansas Museum of Natural History (KU, J. Collins, W. Duellman), Los Angeles County Museum (LACM, R. Bezy, J. Wright), Harvard University–Museum of Comparative Zoology (MCZ, P. Alberch, J. Rosado), Kerr Wildlife Management Area, Kerrville, Texas (KWMA), Louisiana State University–Museum of Zoology (LSUMZ, D. Rossman), Midwestern State University (MU, F. Stangl), National Museum of Natural History (USNM), R. McDiarmid, R. Reynolds, G. Zug), New Mexico State University (NMSU, J. Lapointe), San Diego Natural History Museum (SDNHM, G. Pregill), Southern Illinois University (SIUC, R. Brandon, M. Morris), Southwestern Research Station, Portal, Arizona (SWRS, W. Sherbrooke), Staatliches Museum für Tierkunde (MTKD, F. Obst), Sul Ross State University (SRSU, J. Scudday), Texas A&I University (TAIC, A. Chaney, S. Smith), Texas A&M University–Texas Cooperative Wildlife Collections (TCWC, M. Retzer, K. Friend), Texas Tech University Museum (TTU, C. Jones), Tulane University (TU, H. Dundee), University of Arizona (UAZ, G. Bradley, C. Lowe), University of California at Berkeley–Museum of Vertebrate Zoology (MVZ, D. Good, H. Greene), University of Florida–Florida State Museum (FSM, D. Auth), University of Idaho–Museum of Natural History (UIM, R. Wallace), University of Illinois–Museum of Natural History (UIMNH, L. Maxson), University of Michigan Museum of Zoology (UMMZ, A. Kluge), University of New Mexico–Museum of Southwestern Biology (UNM, H. Snell), University of Northern Arizona–Museum of Northern Arizona (MNA, D. Howard), University of Oklahoma–Stovall Museum (UO, J. Krupa), University of Southwestern Louisiana (USL, J. Jackson), University of Texas–Texas Memorial Museum (TNHC, R. Martin), University of Texas at Arlington (UTACV, J. Campbell, J. Darling), University of Texas at El Paso (UTEP, C. Lieb), University of Utah (UU). In particular, we would like to thank J. V. Vindum (CAS) for calling our attention to four recently accessioned specimens from Mexico in his care. We thank José Luis Villarreal B. for translating the abstract. This research was funded by the Texas Agricultural Experiment Station and a Texas A&M University Faculty–Staff minigrant.

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APPENDIX 1

Specimens Examined

(See Acknowledgments for explanation of museum abbreviations)

Masticophis taeniatus. — UNITED STATES: ARIZONA: Apache Co., Chinle (MCZ 8972), Concho (SDNHM 44192), 1 mi S Hat (UNM 11976), Petrified Forest National Park (UTACV 14342), 2 mi N Springerville (BYU 16673), 4 mi E St. Johns (MVZ 9327), 4 mi S St. Johns (UAZ 39492), 11 mi S jct US 666 & AZ 61 (UAZ 27270); Cochise Co., 8 mi S. Willcox (NMSU 1965); Coconino Co., no

locality (FMNH 25721, UAZ 25726), Bright Angel Canyon (UAZ 25716–25717), Buckfarm Canyon (MNA Z7.2405), Coal Mine Canyon (CA 15905), Glen Canyon (UAZ 39719), Grand Canyon (AMNH 63857, 97792, MNA Z7.2827, SDNHM 3158–3159, USNM 50953, 239259–239260), 22 mi S Cameron (MVZ 25484), Coleman Lake (MVZ 29083), 13 mi N Deadman's Flat (MZ 8680), 11 mi E Desert View (UAZ 34753), Flagstaff (LACM 27773), 17 mi ENE Flagstaff (MNA Z7.624), 28 mi N Flagstaff (BYU 22113), 3 mi N Fredonia (UAZ 25723), 5.7 mi S Fredonia (UAZ 25731), 14 mi E Jacob Lake (CA 10123), 42 mi SW Kayenta (CM 66657), Oak Creek (CAS 35235), Rainbow Lodge (MVZ 17885), San Francisco Mtns (MNA Z1.44), 15 mi E Seligman (LACM 20592), 10 mi N Sunset Crater National Monument (UTEP 4123), 15 mi N The Gap (SM 3961), 12 mi SE Tuba City (CAS 156190), 19 mi SE Tuba City (AMNH 114528), 24.7 mi SE Tuba City (UAZ 25720), Two Guns (SDNHM 32324), Wupatki National Monument (INHS 6500, LACM 20591, MNA Z7.5, Z7.656), 2.6 mi N US 89 on alt US 89 (UAZ 25730); *Gila Co.*, no locality (USL 8946), Crook National Forest (UIMNH 72093), 11 mi N Miami (FMNH 106182–106283), Pine (BYU 11291), 3 mi NW Pine (CA 17900), Pioneer Peak S of Globe (UIMNH 72092), Pinal Mtns (UAZ 25722), 8 mi W Roosevelt (UAZ 25725), Roosevelt Reservoir (USNM 105228), 4.3 mi S Rose Creek Campgrounds (UIMNH 72094), Rose Creek Lodge (MVZ 49918), near San Carlos (CM 26675), Sierra Ancha Experimental Forest-SAEF (CM 53796), SAEF T4.5N R21E Sec 31 (ASU 10534–10535), 7 mi SE SAEF Headquarters (ASU 11299), Carris Ranch in SAEF (MVZ 6309), Tick Flat (ASU 10533), 6.8 mi N Young (UAZ 35973); *Graham Co.*, Graham Mtns (USNM 51764), 7.5 mi E Klondyke (AMNH 111226), San Carlos Indian Reservation (CAS 158216–158217), Santa Teresa Mtns (SDNHM 62706); *Greenlee Co.*, Blue Mtns (UNM 22319–22320), 40 mi NW Clifton (UAZ 25724), 7 mi SW New Mexico state line on AZ 78 (UNM 33141); *Mohave Co.*, Cerbat Mtns (UAZ 40571), 7.6 mi E Hackberry (MVZ 170750), 16.3 mi S & 9.5 mi E Hackberry (UAZ 25734), Hualpai Mtn Park (TCWC 9341), 32 mi E Kingman (MVZ 175138), 35 mi W Kingman (TCWC 9340), Mt Trumbull (UAZ 25719), 11.8 mi E jct US 40 & AZ 93 on US 40 (LACM 135203), 8.2 mi W jct Main St Valley Rd & Virgin Mtn Rd (UAZ 25715), 15.1 mi E jct Main St Valley Rd & Navajo Trail (UAZ 25718), 13.5 mi E Yucca (MNA Z7.656); *Navajo Co.*, 12 mi W Cibecue (MCZ 101217), New Orabi (AMNH 110454, UAZ 25727), Paiute Canyon (MVZ 17884), S of Taylor (BYU 13599); *Pinal Co.*, SE Superior (UIMNH 72095); *Yavapai Co.*, Bradshaw Mtns (AMNH 63978), 9.8 mi NW Congress (UIMNH 71995), Cottonwood (ASU 208223, CM 66655, FMNH 208223), 4 mi SW Cottonwood (CM 66656), Granite Dells (UAZ 9333–9334), 3 mi W Iron Springs (UAZ 25732), Milk Creek (UAZ 25728), Mingus Mtn (CM 66660), 1 mi N Montezuma's Castle National Monument (EAL 3084), Peeples Valley (UIMNH 72096), Prescott (ASU 1614, UAZ 25729, USNM 15704), 12 mi SW Prescott (AMNH 126735), 13.6 mi NNE Prescott (CM 66659), 4 mi W Sedona (UIMNH 43200), 7 mi W Sedona (CM 66661), Whipple (MCZ 5865, USNM 11422–11423), Yarnell (CA 3151, SDNHM 32325), 1 mi S Yarnell (SDNHM 5290), 6 mi N Yarnell (CA 3468); *Yuma Co.*, 3 mi S & 6.2 mi W Gladden (UAZ 25735), Kofa Mtns (UNM 41621, USNM 221843–221844). **CALIFORNIA:** *Alameda Co.*, near Oakland (CAS 10639); *Inyo Co.*, Argus Mtns (SDNHM 17061), 18 mi N Cowhorn Valley (SDNHM 48083), 5 mi W & 1.25 mi S Independence (MVZ 38410–38411), 6 mi W Independence (AMNH 110680); Panamint Mtns (MVZ 19256, 64131); *Lassen Co.*, 9 mi E Amedee (MVZ 24579), Bare Creek Ranch (LSUMZ 8802–8803), Fort Sage Mtn (MVZ 20481), Lassen National Park (MVZ 68313), 5 mi E Litchfield (MVZ 36136), 6 mi E Susanville (UMMZ 91821); *Modoc Co.*, 6 mi N Eagleville (LSUMZ 8804); *Mono Co.*, 2 mi S Benton (MVZ 3714), between Hot Creek & Mammoth Jct (CAS 8395), near Hot Creek geysers (SDNHM 19357–19360), Sierra Nevadas (LACM 2270), Topas Lake (SDNHM 28860), Whitmore Tubs (SDNHM 34240); *San Bernardino Co.*, Chemehuevi Mtns (LACM 2272–2274), Clark Mtn (MVZ 28564–28566, 41703), 11.2 km S Lima (MVZ 100271), Midhills Campground (MVZ 150189); *Siskiyou Co.*, Ash Creek at Klamath River (UNM 26436), 3 mi S & 1 mi E Capco (MVZ 85073), Gazelle (CAS 36063), 15 mi NE Weed (MVZ 17259). **COLORADO:** *Garfield Co.*, 6 mi N Mesa Co line (UIMNH 80484), 7 mi W Rifle (USNM 40197); *Mesa Co.*, Colorado National Monument-CNM (CM 42791–42792, 43537, SM 13299), Debeque Canyon (CM 43538), Fruita Entrance to CNM (UIMNH 53217), Grand Junction (FMNH 920), Palisade (USNM 29610), Plateau Creek (USNM 40196); *Moffat Co.*, Jct Green & Yampa rivers (UIMNH 64659); *Montezuma Co.*, 6 mi S Cortez (BYU 41686), Mesa Verde National Park (KU 106150–106151, 129712–129714); *Montrose Co.*, Paradox Valley (SDNHM 8680). **IDAHO:** *Ada Co.*, Boise (CAS 41362–41363, KU 8443, UMMZ 63990–63993), Cinder Cone Butte (CAS 64203–64206, FMNH 6963), Snake River SE Melba (SDNHM 1432), Swan Falls near Snake River (TCWC 64836–64837), near Swan Falls (UIM 329 [6]); *Bannock Co.*, Pocatello (KU 6468, 11803); *Bingham Co.*, no locality (MVZ 28765); *Butte Co.*, Arco (BYU 30771); *Cassia Co.*, Albion (UMMZ 71466), Raft River Valley (BYU 42032); *Elmore Co.*, Cleft (CAS 64185, 64207), 4 mi W Hammett (MVZ 21562), 14 mi S Mtn Home (UIM 196); *Fremont Co.*, Yellow Stone (USNM 56018); *Gooding Co.*, 2 mi S Hagerman (MVZ 18302), between Snake River & Bliss (CAS 4065); *Jerome Co.*, Jerome (TCWC 57856); *Owyhee Co.*, 9.8 mi E Bruneau (UMMZ 133006,

133398), W of Homedale (UMMZ 68299), E of Hot Springs & S of Bruneau (SDNHM 1431), Fossil Butte (UIM 390 [2]), 18 mi SW Nampa (BYU 40813), 22 mi N Nevada State Line (MVZ 24580–24581), lower Reynolds (UIM 291 [2]), Squaw Creek (UIM 103), Sucker Creek (CM 91569), Warm Springs Ferry (CAS 55246); *Twin Falls Co.*, SW 0.25 Sec 28 T17S R13E (UMMZ 125687). **NEVADA:** *Churchill Co.*, 90 mi E Fallon (BYU 16650), 8.5 mi SE Hausen (MVZ 21511); *Clark Co.*, 20 mi SW Indian Springs (UNM 4802), 1 mi N Lee Canyon Rd to Charles Mtns (LACM 59025), 10 mi W Hwy 95 on NV 156 (MVZ 182611), Spring Mtns (CAS 2003); *Douglas Co.*, 3 mi NE Topaz Lake (MVZ 18635); *Elko Co.*, Carlin (UMMZ 43123–43127, 43156, 149867–149869), 15 mi W Wendover, UT (CAS 10025); *Esmeralda Co.*, 12 mi E Oasis (KU 82339); *Eureka Co.*, Dunphy (SDNHM 27787, 27851); *Humboldt Co.*, 10 mi SW Denio (KU 109967), 6 mi S Golconda (MVZ 20622), Pine River Mtn (MVZ 1514, 1516), Quinn River Crossing (MVZ 1513, 1515), 5 mi S Quinn River Crossing (MVZ 21515), 2.5 mi N Ryepatch pump station valley (UMMZ 78026), Valmy (SDNHM 27788), 2 mi W Winnemucca (CAS 120818), 10.2 mi SW Winnemucca (UIMNH 4396); *Lander Co.*, Antelope Spring (USNM 8120), 3 mi E Austin (TNHC 7441), 16.5 mi S Battle Mtn (USNM 218839), 19.3 mi SSE Battle Mtn (USNM 218838), Kingston Creek (MVZ 12171), Toquime Range (MVZ 42085), Toiyabe Range (MVZ 42084); *Lincoln Co.*, Caliente (CAS 36976), 0.5 mi E Panaca (MVZ 56917), 13 mi NNW Pioche (MVZ 61816), N end Timpahute (MVZ 14283); *Mineral Co.*, Excelsior Mtns (MVZ 10865), 18 mi SE Hawthorne (SDNHM 37702), 15 mi ENE Luning (UMMZ 124602); *Nye Co.*, Cloverdale (USNM 44525), 2 mi E Garrett Ranch (SDNHM 40654), Mercury (BYU 17409, 18755–18756), Nevada Test Site (MVZ 140912), N Twin River (MVZ 12843, 16180), 0.5 mi S Oak Spring (MVZ 13082), Rainer Mesa (BYU 23858, 30547), Toiyabe Range (UNM 52432), 0.5 E Tonopah (UNM 463), 18 mi E Tonopah (SM 3962), 24.4 mi ENE Tonopah (CAS 21320), S Twin River (MVZ 12170), White River Valley (UMMZ 86127), Wisconsin Creek (MVZ 12841–12842); *Ormsby Co.*, Carson City (CAS 6527, SDNHM 27785, USNM 9520), 4 mi SW Carson City (MVZ 20395); *Pershing Co.*, Humboldt Range (MVZ 21513–21515), Imlay (MVZ 43150), 5 mi E Lovelock (MVZ 11983), 15.3 mi NW Lovelock (SDNHM 37791); *Washoe Co.*, Little High Rock Canyon (MVZ 7546), 6 mi S Pahrump (MVZ 24582), Pyramid Lake (CAS 6526, 40505, 44146–44147, USNM 44536, 50801), 0.5 mi S Pyramid Lake (MVZ 32100), near Reno (KU 6667), 12 mi NNW Reno (CAS 93781–93784), Smoke Creek 1 mi from CA state line (MVZ 20482), Sutcliffe (CAS 22188); *White Pine Co.*, Baker (CAS 14372), 1.7 mi E El Dorado (MVZ 70341), Major Woods (CAS 14371), Mt. Moriah (MVZ 24583), Spring Valley (UMMZ 84911), 8 mi N Yelland's Ranch (SDNHM 19704). **NEW MEXICO:** *Bernalillo Co.*, 3 mi S Alameda (UNM 18254), Albuquerque (KU 5536, UNM 460, 4722, 11407, 12254, 22551, 22562, 33751, 38812), 17 mi E Albuquerque (AMNH 115716), Hwy 10 10.6 mi S US 66 (UNM 32384), Sandia Mtns (UNM 11611, 15600, 18253, 25658); *Catron Co.*, 10 mi N Alma (UNM 33122), 4 mi W Baldy Creek (NMSU 2956–2957), Glenwood Fish Hatchery (NMSU 3734, 4401), 0.9 mi NE Glenwood (AMNH 120697), 1 mi S Glenwood (UNM 4723), 1.3 mi N Glenwood (CM 48768), 2.5 mi N Glenwood (BYU 13979), 4 mi S Glenwood (UNM 18740), 5 mi S Glenwood (KU 6477–6478), 6 mi S Glenwood (AMNH 114035), 6.5 mi S & 0.5 mi W Glenwood (TCWC 65001), 13.5 mi E Glenwood (UNM 11535), 1 mi W Mogollon (UTEP 1711), Nichols Canyon (NMSU 5328), Pleasanton (UNM 32169), 4 mi S Pleasanton (UTEP 1710), San Francisco Hot Springs (UAZ 25714, UNM 38853), Whitewater Canyon (UNM 6794); *Chaves Co.*, Bishops Cap (UTEP 2540), Elk (LACM 20598), Jornada Experimental Range (USNM 102252), 4 mi N Las Cruces (LACM 133881), 8 mi N Las Cruces (LACM 2279), 11 mi S Las Cruces (DMNH 1930), 11 mi N Las Cruces (LSUMZ 10027), 12 mi N Las Cruces (LACM 2278), 22 mi W & 15 mi N Las Cruces (LACM 133882), 14.9 mi E Mayfield (LACM 20597), 2 mi W & 1 mi S Mesilla (LACM 133883), 5 mi S Mesilla (UTEP 107), Organ Mtns (UTEP 9509), 3.9 mi N Organ (LACM 103360), Picacho Canyon (NMSU 2833), 1 mi S Radium Springs (CU 5056), 1 mi N Radium Springs (NMSU 1984), 1 mi E Rincon (UTEP 7639), 13 mi N & 4.6 mi E University Park (KU 72916), 3.2 mi S US 70 on Aguirre Springs Rd (NMSU 5837); *Eddy Co.*, no locality (UTEP 7660), 30 mi SW Carlsbad (CM 18297), NM 137 W Carlsbad (UNM 37796), Carlsbad Caverns National Park (TTU 3581, UMMZ 121794, 121797–121798, 123477, 125338, UNM 30458, 30926), Dog Canyon Rd 4 mi N TX state line (TTU 9679), Guadalupe Mtns (UMMZ 123470, UNM 25729), Rattlesnake Canyon (KU 8386), Robinson Draw (UMMZ 123473), 1 mi N Whites City (UMMZ 121795–121796); *Grant Co.*, Blue Creek (NMSU 5259), 5 mi NW Buckhorn (UNM 6425), Gertie Canyon in Big Burro Mtns (MVZ 7119), Burro Mtns (NMSU 4694, UTEP 1974–1975), 4 mi S Cliff (NMSU 4391), 4 mi N Cliff (NMSU 3733), 5.5 km E & 6.2 km N Cliff (UNM 37768), 7.5 mi N Cliff (NMSU 4395), 10.5 mi N Cliff (UAZ 35078), 16 mi SW Cliff (NMSU 4392), 16 mi S Cliff (NMSU 4396), City of Rocks State Park (KU 72917), Dwyer (KU 109968), Gila National Forest (UNM 38913), Gila River (NMSU 6019, UNM 461), Hachita (AMNH 85071), 18 mi N Lordsburg (UIMNH 72091), N of Mimbres (CA 5312), 1 mi N Mimbres (UNM 32862, UTEP 7638), 5 mi N Mimbres (UMMZ 79215), Mimbres River Valley (NMSU 4399), Pinos Altos (UAZ 25713), 2.75 mi NNW Pinos Altos (AMNH 84991), Redrock (NMSU 3730), 5 mi NE San Lorenzo (UTEP 1345), Sapillo Creek Bridge (NMSU 4512), 2 mi W Sapillo Creek Bridge

(NMSU 4390), Sawmill Creek (UNM 38932), Silver City (MVZ 42593, NMSU 4397, 4513, 4696–4697), 1 mi S Silver City (UNM 4721), 2.9 mi W Silver City (UTACV 2621), 3 mi S Silver City (NMSU 4493), 10 mi S & 8 mi W Silver City (UNM 15205), 13 mi W Silver City (UNM 15294), 19 mi W Silver City (NMSU 4695), 20 mi S Silver City (TCWC 63047), 25 mi SW Silver City (NMSU 4400), Slades Canyon (NMSU 4394), 1 mi NNE Vanadium (NMSU 4389), 10.7 mi NNE White Signal (UTEP 8763), jct NM 61 & Hwy 90 (LACM 76408), Sec 12 T18S R16W (NMSU 4398), 13.3 mi NE jct NM 90 & US 70 (UNM 32033); *Hidalgo Co.*, Alamo Hueco Mtns (AMNH 78996, UTEP 11355), 4.5 mi NW Antelope Wells (NMSU 1868), 39 mi S Hatchita (ASC 10952), 0.7 mi S Grant Co line (UNM 6793), Little Hatchet Mtns (AMNH 74725, 75410, UTEP 10570), 1.8 mi W jct NM 530 & 92 (NMSU 5347); *Lincoln Co.*, Corona (LACM 2277), 2 mi NW Carrizozo (UMMZ 67658), 4 mi NW Carrizozo (AMNH 111227), 2 mi NW Hondo (UNM 23558), Tularosa Malpais (UNM 37153), 0.5 mi N White Oaks (UNM 31673); *Luna Co.*, 5.7 mi N Columbus (LACM 103361), 21.5 mi W Columbus (TCWC 56339), 19 mi NNE Deming (UTEP 5676), 10 mi NW Florida (NMSU 4514), Florida Mtns (UTEP 200, 11261), 2 mi N Nutt (LACM 109526), Tres Hermanas Mtns (UNM 462); *McKinley Co.*, 5.9 mi N Ya-ta-hey (UTEP 9540); *Otero Co.*, Alamo Mtn NW 0.25 Sec 21 T26S R13E (NMSU 6329), 1 mi NE Alamogordo (NMSU 4698), Dog Canyon (USL 24962), 7.5 mi E LaLuz (LACM 20599), SW 0.25 Sec 33 T17S R10E (NMSU 6186–6187); *Quay Co.*, 9 mi W & 1.5 mi S Tucumari Mtn (UNM 19705); *Rio Arriba Co.*, 14 mi NW Abiqui (UAZ 39721), Nutria (USNM 8432); *Sandoval Co.*, 4 mi S Algodones (UNM 16697), Bandelier National Monument (UNM 30534), 15.2 mi SE Cuba (UNM 22071), Jemez Mtns (UNM 30879), Jemez Pueblo (UNM 459, 4720), Juan Tabo Picnic Area (UNM 10902, 13518, 37797), Placitas (UNM 458, 18255), 2 mi SW Placitas (CM 58692), Sante Fe National Forest (UTEP 8926); *San Juan Co.*, Chaco Canyon National Monument (UNM 3395, 21835–21839), 2.6 mi S Newcomb (UAZ 36364), Shiprock (USNM 2110 holotype, 44503), 4 mi W Shiprock (UTACV 1182), NE 0.25 Sec 24 T32N R7W (UNM 4153), Wool Canyon (UU 3738); *San Miguel Co.*, 1 mi below Conchas dam (UNM 21909), 3 mi below Conchas dam (UNM 18256), 1 mi N Sena (UNM 32863), 7.3 mi SE Trujillo (LACM 20600); *Santa Fe Co.*, 4 mi N Golden (UNM 31669), Jemez Mtns (UNM 364643), 5 mi NE Los Cerillos (UNM 456), 1.5 mi S Madrid (UNM 23514), 2 mi N Madrid (UNM 10243); *Sierra Co.*, Arrey (NMSU 1477), Caballo Dam (UTEP 152), Elephant Butte (LACM 2276), 2 mi N Ft McCrae (NMSU uncatalogued), Hillsboro (UAZ 40319), 0.8 mi W Hillsboro (UTEP 10698), 3 mi W Hillsboro (NMSU 2028), 3 mi S Hillsboro (LACM 76409), 16 mi E Hillsboro (LACM 76417), Hospital Canyon (NMSU 5531), 2 mi N Lake Valley (NMSU 4402), 1 mi N Truth or Consequences (LACM 2275), 3 mi W Truth or Consequences (NMSU 2020), 12 mi N Truth or Consequences (UNM 13730), 1.5 mi W jct NM 52 & 135 on 135 (NMSU 5484); *Socorro Co.*, 2.3 mi E Bingham (UNM 12762), 6 mi E Bingham (LACM 20594), 12 mi SE New Bingham (LACM 20596), Chupadera Mesa (LACM 63453), 15 mi W Carrizozo (UNM 16745), 3 mi E & 3 mi S Dusty (TCWC 66165), 13.5 mi NE Magdalena (UNM 30880, 30895), Magdalena Mtns (UNM 4154–4155, 13855), Mockingbird Gap (LACM 20595), Rio Salado (UNM 14876), 8.9 km W & 1.4 km N I-40 bridge over Rio Salado (UNM 39258), 15 mi S & 3 mi E Rosedale (KU 47791), 25 mi SW San Antonio (UNM 455), 8.7 mi W Socorro (LACM 20593), 16.1 mi W Socorro (UNM 11525); *Torrance Co.*, 9 mi W Mountnair (UNM 457); *Valencia Co.*, 9 mi N Acoma (MVZ 128112), 5 mi E Grants (CU 3052), 6 mi NE Grants (UNM 22332), 8 mi E Grants (UNM 8843), 10.4 mi S Grants (CU 5602), Mesa Encantada (UNM 30896). **OREGON:** *Crook Co.*, no locality (MVZ 26924); *Deschutes Co.*, 3 mi W Terrebonne (UNM 33169), 4 mi W Terrebonne (UNM 30941); *Harney Co.*, Fields (UMMZ 133342, 133379), 3 mi S Fields (UMMZ 133091), 6 mi S Fields (UMMZ 133001, 133092 [3]), Frenchglen (CM 20745); *Lake Co.*, Picture Pass Summit (UMMZ 135986); *Malheur Co.*, 5 mi S Adrian (UMMZ 124574); *Wasco Co.*, Maupin (MVZ 62055); **TEXAS:** *Bandera Co.*, 18 mi NW Medina (TNHC 1904), 6 mi S Tarpley (SM 7491), 13 mi W Tarpley (UNM 37798); *Bexar Co.*, Helotes (SM 228–229), 1 mi N Helotes (MVZ 68462), Helotes Creek (CU 609, SM 6384), San Antonio (UNM 13522, UTEP 9595), 17 mi N San Antonio (AMNH 22743, 74548), 18 mi N San Antonio (CM 22850), 22 mi N San Antonio (CU 1771–1772); *Blanco Co.*, 4.9 mi W Johnson City (USL 1793), 5.7 mi E Johnson City (USL 1792), 17 mi SE Johnson City (TNHC 28913), 20 mi NW Johnson City (MCZ 62561), 16.9 mi E Sandy (LSUMZ 14149); *Brewster Co.*, no locality (SRSU 1469, UMMZ 71925), Alpine (CAS 7503, SRSU 1844, 4587), 10 mi S Alpine (SRSU 1694), 22 mi S Alpine (TCWC 28940), 42 km S Alpine (KU 176790), 32.1 mi S Alpine (LSUMZ 23342), 59.5 mi S Alpine (USL 6799), 65 mi S Alpine (SRSU 1845), Big Bend National Park (AMNH 72527, 77318, 111228, CA 7821, CM 5006, 60005, FMNH 26617–26618, 26803–26804, 27707–27708, 27845, LACM 103362–103363, MVZ 25362, SM 6388–6392, SRSU 3927, 5079, TCWC 16127–16128, 40111, TTU 4, 629, UAZ 34784, 39228, 40391, UMMZ 66026–66029, 72088, 95435, UNM 9025–9026, 18258, 20801, 20891–20893, 22238, 22381, USNM 103638, UTACV 2619), 1 mi N BBNP on Hwy 118 (UMMZ 32386), 13 mi N BBNP on Hwy 118 (UIMNH 47645), Black Gap Wildlife Management Area (DMNH 296, 302, TCWC 12296, TNHC 12603, 12797, 12984), Boquillas (CA 4860), Lajitas (KU 51945), Marathon (SM 5926–5927), 12 mi S Marathon (UMMZ 20827), 12 mi S & 2 mi W Marathon (FWM

6910), 13 mi S Marathon (SRSU 4665), 22 mi E Marathon (MVZ 53916), 31 mi SE Marathon (SRSU 1671), Reed Plateau (TCWC 64999), Rosillos Mtns (FMNH 75480–75482, UMMZ 114344), 25 mi W Sanderson (AMNH 94276), Santiago Mtns (UMMZ 114203), Study Butte (NMSU 3210), 7 mi W Study Butte (NMSU 3211), 10 mi S Study Butte (SRSU 2193), 28.5 km N Study Butte (UTACV 12736), Terlingua Ranch (TCWC 65285), 1.1 mi W jct Hwys 170 & 118 on 170 (TCWC 63376), 4 mi N jct Hwys 118 & 170 on 118 (UTEP 10569), 48.9 mi S jct Hwys 118 & 90 on 118 (TCWC 63378); *Burnet Co.*, Clear Creek (CAS 33072, SM 752), 12 mi W Inks Dam (TNHC 2639), 7 mi NW Marble Falls (TAIC 1414); *Coleman Co.*, 0.25 mi N Santa Anna (UTACV 2620); *Comal Co.*, 1 mi NW Fischer (TCWC 25397), Hunter (UMMZ 74328), New Braunfels (UMMZ 69662), 3.5 mi NNE New Braunfels (MVZ 99224), 5 mi NW New Braunfels (UMMZ 74074); *Concho Co.*, 50 mi SE San Angelo (LACM 74105); *Crockett Co.*, Howard Springs (USNM 1970), 17 mi E Iraan (TCWC 40112), 15 mi W Ozona (UAZ 25757), jct Pecos River & Independence Creek (TU 14472); *Culberson Co.*, Guadalupe Mtns National Park (SM 4881–4882, TCWC 65904, TTU 9675, UMMZ 70134, 123469, 123514, USNM 147878), 6 mi N Kent (MU 4130), 2 mi NE Nickle (KU 72759–72760), Pine Springs (SDNHM 25483), 2 mi W Van Horn (TTU 4741), 15 mi N Van Horn (UMMZ 91474), 25 mi N Van Horn (TCWC 18299–18300); *Edwards Co.*, 0.5 mi W Real Co line on TX 41 (TNHC 44638), 4 mi E Rocksprings (TTU 9715), 7 mi E Rocksprings (UMMZ 102443), 20 mi S Rocksprings (TCWC 65923), 21 mi NE Rocksprings (DMNH 5254), 44.2 km S jct Hwys 290 & I-10 (UTACV 14737); *El Paso Co.*, El Paso (DMNH 2341, 4113, NMSU 5501, UMMZ 74072, UTEP 49, 319–322, 816, 2693, 3368, 3677, 4122, 9073, 10572, 10781, 10804, 11178), Hueco Tanks State Park (UTEP 418, 725, 969, 1043, 1656, 2841, 4369, 10452), 5 mi E Hueco Tanks SP (MVZ 37008); *Gillespie Co.*, 8 mi NE Fredericksburg (TCWC 27390), 10 mi N Fredericksburg (SM 12621), 18 mi N Fredericksburg (TCWC 5204); *Hays Co.*, no locality (ASU 2413), Dripping Springs (TNHC 29046), 4 mi E Dripping Springs (TU 18219), Pollard Wildlife Refuge (TCWC 38792), San Marcos (AMNH 32412), 12 mi WNW San Marcos (SIU-C 226), 15 mi WNW San Marcos (UMMZ 105236), 17 mi NW San Marcos (FSM 56659), Wimberley (FMNH 55049, UTACV 1582), 3 mi S Wimberley (LSUMZ 5852), 7 mi SE Wimberley (TCWC 19030–19031), Wren Ranch Blanco River (FMNH 38061); *Hudspeth Co.*, Eagle Mtns (UTACV 2361, UTEP 1937), 4.5 mi S Hilltop (SRSU 1559), 9.6 mi W Indian Hot Springs (SRSU 4336), Quitman Mtns (UTEP 7455), Sierra Blanca (UTACV 591), 9 mi W Sierra Blanca (KU 40335), 8.2 mi W Van Horn (UTEP 11171); *Jeff Davis Co.*, no locality (NMSU 5838), 14 mi NW Alpine (FSM 56661), 15 mi NW Alpine (SRSU 1846), 29.4 mi NW Alpine (FSM 56660), Davis Mtns (FSM 2530, SM 11532, SRSU 1506, TAIC 4870, TCWC 612, UMMZ 49975–49976, 52925, 81978, UTEP 6812, 10497, 10735), Davis Mtns State Park (AMNH 115717, NMSU 3186, SM 13273), Ft Davis (SRSU 1849–1850, USNM 1971 holotype), 3 mi N Ft Davis (UMMZ 69666), 14 mi N & 8 mi E Ft Davis (KU 56236), 16 mi W Ft Davis (TNHC 7044), 20 mi NW Ft Davis (FSM 56662), 1 mi S Kent (SRSU 1973), 8.5 mi S Kent (UTACV 2701), 3 mi NW McDonald Observatory Rd on 118 (UNM 37799); *Kendall Co.*, Boerne (SM 1901), 11 mi N Boerne (TTU 52), Kendalia (LSUMZ 40055); *Kerr Co.*, 3.6 mi W Hunt (UTACV 2618), 5 mi W Hunt (TCWC 199), 12.9 mi from Hunt (TCWC 47133), 8 mi SW Ingram (TCWC 198), 8.3 mi S & 2.5 mi W Kerrville (TNHC 11933), 10 mi W Kerrville (TCWC 197), 13 mi S Kerrville (TAIC 1058, 1330, 1839, 2618), 17 mi NW Kerrville (TU 14496), 25 mi W Kerrville (UTACV 2194), Kerr Wildlife Management Area (KWMA 1 specimen, TCWC 19033, 25396); *Kimble Co.*, no locality (SRSU 1851), 3.8 mi N Cleo (SM 12620), Crow Ranch (TCWC 65287), Junction (TCWC 64809, 65284), 6 mi W Junction (KU 61061), 10 mi E Junction (MU 3040), 10 mi W Junction (TNHC 29049), 10 mi NNW Junction (TTU 6048), 12 mi NE Junction (SRSU 1852), 15 mi NW Junction (ASC 8130), US 290 SW corner of county (LACM 66805), 1.5 mi W Telegraph (TAIC 3050); *Llano Co.*, 12.8 km S Cherokee (TCWC 63772–63773, 63876, 64841, 65000, UTACV 11126), Enchanted Rock State Natural Area (AMNH 74547, MVZ 128100, TNHC 4498, 4501, 4503, 29048, TU 13549), S of Llano (TNHC 29045), 2.5 mi W Llano (TNHC 12290), 3 mi W Llano (TCWC 64996), 6 mi SW Llano (UTACV 508), 8 mi E Llano (TCWC 64996), 9 mi N Llano (TCWC 531), 19.2 km NNE Llano (UTACV 14738), 19 mi SW Llano (TCWC 58488–58489); *Mason Co.*, 1 mi E Katemcy (ASC 10549), 2 mi WNW Katemcy (ASC 10813), 3.2 mi WNW Katemcy (ASC 10205), 9 mi SE Mason (ASC 386), 9.1 mi W Mason (TCWC 40110), 10 mi W Mason (TCWC 8734), 12 mi S Mason (TCWC 33797), 12 mi NE Mason (TCWC 3298), 13 mi W Mason (SM 11531), 20 mi ESE Mason (TCWC 31125), Olga Zesch Ranch (TCWC 31126); *McCulloch Co.*, S Brady at San Saba River (FSM 3174), FM 734 at San Saba River (TCWC 19032), 2 mi N San Saba River on Hwy 71 (TCWC 64838); *Medina Co.*, Rio Medina (CM 19919), Hwy 173 at Verde Creek (TCWC 63775); *Menard Co.*, 2.5 E Menard (TCWC 38015), 3 mi E Menard (TCWC 42362), 10 mi W Menard (SM 8951), 10 mi SW Menard (TNHC 12262); *Mills Co.*, 15 mi SSW Goldthwaite (TNHC 14101); *Pecos Co.*, ANSP 15621, 15654, 17076; LACM 66802 15 mi E Ft Stockton; TCWC 27383 13 mi E & 1 mi N Bakersfield; UNM 12079 Huckabee Ranch; *Presidio Co.*, 8 mi NE Candelaria (TCWC 27637, 27639–27643), 9 mi NE Candelaria (TCWC 27639), 24 mi SW Ft Davis (TTU 4290), Kingston Hot Springs (TCWC 64810–64811), 3 mi W Lajitas (AMNH 112229), 12.1 mi W Lajitas (TCWC

65286), 20.2 mi W Lajitas (TCWC 64324), Madera Canyon N Hwy 170 (SRSU 3931), 16 mi S Marfa (TCWC 30516), 63 mi S Marfa (TNHC 14975-14978), 3 mi E Porvenir (FMNH 46037), 15 mi E Porvenir (TNHC 3589), 1 mi SE Presidio (TCWC 27892), 3 mi SE Presidio, (TCWC 27893), 7 mi E Presidio (ASC 10379), 12 mi N Presidio (SRSU 1848), 16.5 mi N Presidio (SRSU 2298), 29.9 mi N Presidio (CM 60598), 7 mi SE Redford (TCWC 27894), 7.3 mi SE Redford (USL 6834), 12.8 mi SE Redford (TCWC 40112), 13 mi SE Redford (SRSU 3561), 13.5 mi SE Redford (TCWC 26171), 17.5 mi SE Redford (LSUMZ 28669), 7 mi N Ruidosa (SRSU 1972), 4.5 mi S Shafter (UTEP 2773), 6.8 mi SW Shafter (LSUMZ 23332), 13 mi N Shafter (DMNH 4227), 19 mi N Shafter (SRSU 4733), 9 mi W jct US 67 & FM 170 on 170 (TCWC 29375), 23.2 mi E jct US 67 & FM 170 on 170 (TCWC 63377), 11 mi W Valentine (TNHC 2851, 3528, 3819, 3837, 3914, 4042, 4262, 15299, 17899); *Reagan Co.*, 9 mi W & 11 mi S Big Lake (ASC 9572), 9 mi S & 12 mi W Big Lake (TCWC 31376); *Real Co.*, 4.5 mi S Leakey (CM 42793), Prade Ranch (FMNH 55018-55019); *Reeves Co.*, Toyahvale (TNHC 1927); *San Saba Co.*, 2 mi W Bend (FWM 5219), 6 mi SE Bend (ASC 385, 5195), 11 mi NW Bend (FWM 5460-5461), 17.5 mi W Lampasas (UTACV 5571), near San Saba (TCWC 20170-20171), 11 mi SW San Saba (FWM 1759-1760), 12.1 mi SE San Saba (FWM 6061), 18 mi NNW San Saba (TNHC 11985-11896); *Sutton Co.*, E of Sonora (LACM 66804), 4 mi S Sonora (KU 82337), 14.9 mi WNW Sonora (UTEP 113); *Terrell Co.*, Chandler Ranch (SRSU 1732, 1971, 1974), 7 mi N Dryden (MU 3897), 8.8 mi W Dryden (UTEP 9156), 21 mi N Dryden (MU 3042), 30 mi W Dryden (SRSU 1975), 20 mi W Langtry (KU 82338), 2 mi W Sanderson (SRSU 3016), 4.7 mi W Sanderson (TAIC 4352), 5.7 mi W Sanderson (UIMNH 34274), 7.9 mi W Sanderson (UTEP 9051), 7 mi SW Sheffield (TTU 2530), 10 mi S Sheffield (TNHC 7994), 13 mi S Sheffield (TNHC 7681), 21 mi S Sheffield (TNHC 8225), 25.9 mi S Sheffield (TCWC 28885), 30 mi S Sheffield (TNHC 7838); *Throckmorton Co.*, 15 mi SW Throckmorton (TNHC 26579); *Travis Co.*, no locality (LACM 103364), Austin (AMNH 4191, FSM 11989, TNHC 35221, TTU 86), NW of Austin (TNHC 26828), 7 mi SW Austin (FSM 56656-56658), 8 mi NW Austin (TNHC 2069), 10 mi N Austin (AMNH 122738), 12 mi W Austin (TNHC 19651, 20493), 15 mi SW Austin (TNHC 4497), 17 mi NW Austin (TNHC 4500), 18 mi NNW Austin (TNHC 4499), 20 mi NNW Austin (TNHC 4502), 20 mi W Austin (UIMNH 2652-2654), Gaines Ranch (TNHC 1847, 4897, 9084, 12295, 15295, 20542), Hamilton's Pool (LACM 66801), near Lake Travis (TCWC 20239), old river above Winfree (TNHC 29050), RR 620 1 mi W jct with RR 2769 (UAZ 25758), US 290 E of Hays Co line (FSM 7801-7802); *Upton Co.*, 24 km WNW Rankin (UTACV 14472-14474); *Uvalde Co.*, 3.2 mi S Nueces River on Hwy 55 (TCWC 64840), 8.2 mi N jct Hwys 1275 & 1835 (USL 19742); *Val Verde Co.*, Caulk Ranch (TAIC 3217), Comstock (TNHC 29047), N of Comstock on Pandale rd (Taic 4780), 1 mi W Comstock (ASC 9570, UAZ 40392), 1.5 mi SE Comstock (ASC 9568), 6.2 mi W Comstock (LSUMZ 23331), 7.9 mi NW Comstock (ASC 9565), 8 mi SW Comstock (USNM 32782), 15 mi SE Comstock (ASC 9564), 16.6 mi N Comstock (ASC 9571), 17 mi SE Comstock (ASC 9567), 18 mi SE Comstock (ASC 9569), 19 mi NE Comstock (TNHC 32512), 21.6 mi N Comstock (TNHC 32530), 7 mi NW Del Rio (UTACV 1339), 17 mi W Del Rio (MU 3041), 18 mi N Del Rio (CAS 103476), 18 mi NW Del Rio (SRSU 1843), 25.2 mi N Del Rio (UNM 8848), 36 mi NNW Del Rio (ASC 1524), 36.3 mi N Del Rio (UNM 8325), 40 mi N & 30 mi W Del Rio (ASC 5763), Devils River (USNM 32781), Evans Creek at Lake Amistad (SRSU 2746), 16.6 mi S Everett's Crossing (TAIC 4283), Fawcett Ranch (SRSU 3457, 3414, TTU 4355), 13 mi W Juno (ASC 9566), 2 mi W. Langtry (KU 61062), 7 mi N Langtry (TAIC 3558), 8 mi W Langtry (CM 88738), 20.9 km N Langtry (UTACV 14613), 25 mi N Langtry (TAIC 4118), 35 mi N Langtry (TAIC 3465 [3], 3476, 3498, 3556-3557, 3560, 3984), 29.8 mi W Loma Alta (TCWC 13837), Pandale hwy jct (TAIC 3540), 7.1 km S Pandale (UTACV 16341), mouth of Pecos River (UMMZ 74335-74336), Pecos River at Lake Amistad (SRSU 4812), US 90 at Pecos River (TAIC 1915, 2423, TCWC 33796, UMMZ 92798), US 90 2 mi W Amistad Dam (TAIC 2364), 1 mi W Shumla (TNHC 35223), Hwy 163 29 mi N jct with US 90 (UMMZ 175826), US 90 9 mi ESE Terrel Co line (UTEP 10576); *Williamson Co.*, 3 mi N Georgetown (UTACV 1340). **UTAH:** *Beaver Co.*, Baker's Canyon (USNM 36346), Beaver Creek hills (AMNH 29367-29368), Milford Valley, (BYU 564, 1640-1641), 50 mi W Milford BYU 563, 1637, 1809), White Sage Valley (SDNHM 40691); *Box Elder Co.*, Locomotive Springs (UU 917-918, 2000-2004, 8062), 22 mi N Wendover (BYU 42416); *Carbon Co.*, 25.3 mi S & 20 mi W Ouray (AMNH 112918), Price (BYU 2792, KU 82340, UU 1368, 1409-1410), 3 mi W Price (BYU 22951); *Davis Co.*, Antelope Island (LACM 121003), Farmington (AMNH 14231); *Duchesne Co.*, Montwell (BYU 16719), 5 mi W Roosevelt (BYU 16718); *Emery Co.*, Morrison Salt Wash 10 mi W Green River (AMNH 64840), San Rafael (BYU 2906), upper Temple Mtn (BYU 18997), 6 mi N Temple Mtn (BYU 20732), 2 mi NW Temple Jct (BYU 16614), Woodside (BYU 258), 2 mi NNE Jct Hwy 24 & road to San Rafael Swell (CAS 92465); *Garfield Co.*, Hog Springs (UTACV 12737), 4 mi NW Hog Springs (BYU 12694), 1 mi W Star Springs (BYU 12623); *Grand Co.*, Arches National Park (AMNH 115603, BYU 13036), near Castleton (LACM 103365-103366), 2 mi NW Castleton (UMMZ 68588), 25 mi N Cisco (FMNH 33909), 12 mi SE Crescent Jct (BYU 30533), near Colorado state line (KU 5533), Green River (BYU 257), 2 mi S Moab

(UMMZ 68587), 5 mi N Thompson (UMMZ 68586); *Iron Co.*, Antelope Springs (SDNHM 40662), Cedar City (BYU 392), 1 mi N Cedar City (KU 20906–20907), Sulphur Springs (SDNHM 40661); *Juab Co.*, 18 mi S & 9 mi W Eureka (CM 91197), 20 mi W Nephi (UIMNH 2135), Yopaz Mtn (BYU 9072); *Kane Co.*, 10 mi S Alton (BYU 11312), Glen Canyon (UAZ 39720), Kanab (UAZ 25759), 3 mi N Kanab (UMMZ 73390), 7 mi N Kanab (MNA 7.254), 19 mi E Kanab (BYU 8715), Kaiparowits Plateau (UU 1288, 1606), Orderville (SDNHM 25485), Piaria (BYU 2893); *Millard Co.*, Cove Fort (CAS 54150), 3 mi N Cove Fort (BYU 568), 20 mi NW Delta (SDNHM 674–675), 30 mi N Delta (CU 1082, SDNHM 1274), 65 mi W Delta (UIMNH 2132–2134), Fillmore (MCZ 13361–13362), 2 mi N Fillmore (UMMZ 70654), 10 mi NW Fillmore (UMMZ 70652), 10 mi SW Fillmore (UMMZ 70653), 10–11 mi W Fillmore (UMMZ 70655), 20 mi W Hinckley (BYU 16590), 7 mi S Kanosh (CAS 47756), Maple Grove Forest Canyon (UU 3386), 18.1 mi E NV state line (CM 49031); *Piute Co.*, 8.4 mi N Circleville (ASU 21199), 4.4 mi S Marysville (LACM 20590); *Salt Lake Co.*, 0.5 mi from mouth of Emigration Canyon (UU 14167), Fort Douglas (CAS 14167, 30923–30924, 38761), Salt Lake City (CU 3500, MCZ 8899, 9051, 9053); *San Juan Co.*, no locality (FMNH 25274, 25450, 25452, 25712, UTEP 5456), Bluff (AMNH 4871), 6 mi SW Bluff (CM 66658), Devils Lane near Needles (LACM 103367), Indian Creek (BYU 21709–21710), 6 mi W La Sal (BYU 18579), 25 mi SE La Sal (LACM 29037), 12 mi S Moab (UNM 6695), 36 km S Moab (KU 191935); *Sanpete Co.*, Ephraim (UU 89), Maple Canyon (UMMZ 64681); *Sevier Co.*, Monroe (SDNHM 38275); *Tooele Co.*, 13.8 mi N Bonnaville Station (UU 5656–5657), 10 mi W Castle Cliff (CM 53604), Dugway Proving Ground (BYU 14823), 9 mi N Dugway Proving Ground entrance (LACM 103368), Gold Hill (BYU 2998), near Grantsville (UU 2478, 2482), W of Grantsville (UU 1966–1967), Lone Rock Skull Valley (LACM 121038–121080, MVZ 197596), between Ophir & Mercur (UU 2032), Stansbury Island (DURC 379 [2], LACM 121004, UU 1607), Stockton (SDNHM 24679), Tooele (UU 38), W of Vernon (UU 1219a, 8115), Wendover (LACM 24680), 14 mi N & 9 mi E Wendover (UU 3253); *Uintah Co.*, Dinosaur National Monument (BYU 10028), near Jensen (USNM 66196), LaPoint (MVZ 30256), 7 mi E Myton (KU 56097), Oil Town (BYU 22479), 10.6 mi S & 12 mi W Ouray (AMNH 112917), 29 mi S & 19 mi W Ouray (AMNH 112919), near Vernal (CM 7527), 10 mi N Vernal (MVZ 30255), 10 mi W Vernal (MVZ 30254), White River (CM 1430); *Utah Co.*, 3 mi S Allen Ranch (BYU 13042), Cedar Valley (BYU 216, 110, 1109, 14686–14687), Chimney Rock Pass (BYU 2842, 14685), Dividend (BYU 247), mtns W of Elberta (BYU 22093), 5 mi SW Goshen Bay (UIMNH 23875), Lake Mtn (BYU 386), W of Lehi (BYU 2779, 14684), Meseda Bench Prospect (BYU 14986), W of Meseda (UIMNH 34771–34772), Provo (FMNH 41680, UO 3687, USNM 8122), Rock Pile (BYU 30431), near Springville (AMNH 122735), Tintic (BYU 2031–2034, 2136, 2714), Utah Lake (LACM 121081, UU 881); *Washington Co.*, 16 mi NW St. George (USNM 44268), Snow Canyon (BYU 18967), Zion National Park (AMNH 63965, 64141, BYU 215, 394, 1098, 1399, 8739, CAS 56714, DMNH 4276, LACM 132466, SDNHM 3160, UU 74, 341, 805); *Wayne Co.*, no locality (FMNH 62895), Hanksville (BYU 8391–8392); *Weber Co.*, Ogden (MCZ 4595, USNM 10716); *County unknown*, no locality (ANSP 5363, MCZ 1943, USNM 14002), near Casisson, Colorado (KU 6668), Rush Lake (USNM 81244); **WASHINGTON:** *Walla Walla Co.*, 3 mi E Walla Walla (UMMZ 56952–56953). **MEXICO:** **CHIHUAHUA:** no locality (USNM 14272), 18.1 mi E Aldama (UNM 34249), 26.6 mi E Aldama (UNM 34248), 4.5 mi N Hwy 16 on E Colonias Access rd to Aldama (UNM 34250), 4.3 mi E jct Hwy 16 & 45 on 16 (UNM 34251), 18.6 mi W El Ancon (UAZ 35018), 13.6 mi N Ascensión (UAZ 36562), 5 mi N Camargo (UMMZ 117765), 5 km SW Chihuahua (CM 60003), 9.8 mi NW Chihuahua (UIMNH 46021), 30 km N Chihuahua (SDNHM 49501), 72 mi N Chihuahua (UTEP 4097), Coyame (UAZ 35017), 23.2 mi ENE Coyame (EAL 3489), Falomir (UIMNH 52432), 5 mi N Falomir (UIMNH 52433), 30 mi SW Gallego (MVZ 66116), 50 mi E General Trias (UNM 34247), 6 mi NE Janos (UTEP 4228), 5.2 mi S La Mula (SRSU 2816), Lago Santa Maria (USNM 46594), 30 mi N Las Delicias (CM 60006), Norogachi (AMNH 73752), 100 mi SSW Ojinaga (DMNH 2273), 13 mi N Pachera (MVZ 59286), Santa Barbara (AMNH 68193–68198, 68251, 68947–68950), rd to Santa Clara 12 mi from Hwy 45 (UTACV 4532), Sierra del Nido (MVZ 68873, 71014, 73053, UTEP 2519), 2 mi N Yepomera (UAZ 34783), 11.4 mi N Yepomera (UAZ 34425). **COAHUILA:** 3 mi E Americanos (KU 39567), Cuatro Cienegas (USNM 248109), 3 mi S Cuatro Cienegas (AMNH 77315), 3 mi W Cuatro Cienegas (TNHC 33012), 11 km SW Cuatro Cienegas (LACM 116256), 14 km S Cuatro Cienegas (CM 48192), del Carmen Mtns (FMNH 25300), 1 mi E tip San Marcos Mtns (KU 80282), San Pedro (MCZ 4582), 5 mi S San Pedro (USNM 105300), 11 mi N Zapata (UIMNH 48148). **DURANGO:** 8 mi W Durango (AMNH 102520), 84.8 mi W Durango (TCWC 33798), 41 mi E El Verfel (UTACV 8361), 27.5 mi S jct hwy 30 & 45 at La Zarca (UNM 33474), 3 mi SW Lerdo (AMNH 67326–67328), 13.3 mi W Mapuni (UTEP 7749), 4 mi E Metates (UTEP 9374), 3.8 mi NE Pedriceña (TCWC 44007), 6 mi NE Pedriceña (UIMNH 17857), 12 mi S Villa Ocampo (AMNH 86000). **JALISCO:** 8.1 mi ESE Tepetatillo (CAS 165260). **ZACATECAS:** 4 mi W Colorado (FMNH 106181), Sierra Organos (CAS 165223).

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E Christine (SM 1760), 10 mi W Jourdanton (SDNHM 30412), 3.1 mi SE Kyote (TAIC 2229), Lytle (UIMNH 6299), near Pleasanton (TNHC 28758), 6 mi S Pleasanton (UMMZ 71341–71342), 9 mi E Pleasanton (CM 8457), 7 mi E Poteet (UMMZ 74068–74069); *Bee Co.*, Beeville (CA 10838–10840), 1 mi E Beeville (TNHC 28031), 6 mi S Berclair (TNHC 20403), 3.8 mi N Skidmore (TNHC 24445), Tulsita (TNHC 15294); *Bexar Co.*, San Antonio (ASC 4790, CM 16761, UMMZ 74071, UTEP 9931), near San Antonio (SDNHM 20970), 12 mi S San Antonio (UMMZ 74066), 12 mi S San Antonio (UMMZ 74330–74332), 16 mi E San Antonio (UMMZ 74327), 20 mi SW San Antonio (FMNH 108658), 20 mi S San Antonio (UMMZ 74070), Somerset (CM 19911); *Cameron Co.*, no locality (FMNH 38037), Brownsville (AMNH 24991, ANSP 22253, CAS 55354–55355, CU 1199, 1261–1262, FMNH 27170, KU 8393, MCZ 17998–18000, 46506, 15173, 62561 paratype, TCWC 65282, UIMNH 43493 paratype, UMMZ 57681 holotype, 57682–57684 & 57686–576894 paratypes, 59036, 60873–60876, USNM 75981, 84041, UU 1093–1095), 5 mi E Brownsville (TTU 5231), 10 mi NE Brownsville (UMMZ 74065), 12 mi NE Brownsville (UMMZ 74062–74064), 20 mi NE Brownsville (UMMZ 74073), 25–30 mi NNE Brownsville (AMNH 122736–122737), Harlingen (KU 8395), E Laguna Atascosa National Wildlife Refuge (LACM 59023), S Laguna Atascosa NWR (TCWC 61778), 33 mi NW hqrs Laguna Atascosa NWR (USNM 238845), Laguna Heights (TAIC 4987), 3 mi NE San Benito (MVZ 78363), 3 mi S jct FM 106 & 1847 on 1847 (UTACV 8392); *Duval Co.*, 3.9 mi NE Benavides (LSUMZ 23333, 23337), 8.8 mi SW Benavides (23336), 1 mi W Freer (TAIC 2355), 1 mi N Freer (UMMZ 114405), 13.9 mi NE Freer (UMMZ 126173), 1.6 mi NE Realitos (LSUMZ 23339), 1.9 mi NW Realitos (LSUMZ 23334), San Diego (LSUMZ 23338, 23340), 7.9 mi SW San Diego (LSUMZ 23335), 4.7 mi jct 1329 & 2295 on 2295 (TAIC 3328 [2]); *Frio Co.*, Dilley (UTACV 293), 7 mi NW Dilley (TCWC 63774, 63919), 3.7 mi SW Moore (TNHC 47670), Hwy 57 at Frio River (USL 15084); *Goliad Co.*, 8 mi E Goliad (TNHC 17900, 17930); *Hidalgo Co.*, Alamo (USNM 159384), Edinburg (AMNH 74549–74551, CA 6350–6351), N of Edinburg (CU 589), 1 mi N Edinburg (TCWC 18301), 12 mi W Hidalgo (TCWC 65283), 13 mi N Edinburg (TCWC 36389), 19 mi S Encino (UIMNH 3832–3833), 14.7 mi NW La Joya (SM 8949), 6 mi S Linn (SRSU 1220), 6 mi S McAllen (TNHC 9059), 1 mi W Red Gate (TAIC 4666), 1 mi W jct FM 2984 & 676 (TAIC 1474); *Jim Hogg Co.*, 9.3 mi N Guerra (TCWC 60755), 2 mi S Randado (TAIC 4398), 5.8 mi S jct Hwys 3973 & 649 on 649 (TCWC 48658); *Jim Wells Co.*, Alice (TTU 791), 1.5 mi E Alice (UMMZ 69663), 3 mi S Ben Bolt (LSUMZ 13288), 5 mi S Ben Bolt (TNHC 23169), La Copita Experimental Ranch (TCWC 63408, 64389), 3 mi N Premont (UIMNH 16874), 10.9 mi N Premont (SM 8950); *Kenedy Co.*, 9 mi S Armstrong (TNHC 28003), 15.6 mi Armstrong (TAIC 3037), 12 mi S Norias (KU 61063), 10.2 mi S Riviera (FSM 43495), 5.7 mi S Sarita (TAIC 3099), 6 mi S Sarita (UTACV 16827), 8 mi S Sarita (LSUMZ 27724); *Kleberg Co.*, Laureles Division King Ranch (TAIC 5307), Kingsville (CAS 103473–103474, EAL 5000, TAIC 203, 361, 1707, 1731, 1942, 1976, 2059, 2073, 2382, 3563, 4255, 4772, 4857, 5257, 5307, 5364), 8.5 mi S Kingsville (TAIC 693 [2], 924, 2069), 2.5 mi S Riviera (TNHC 28030), 8 mi E Riviera (TAIC 933), 0.5 mi W Riviera Beach (TAIC 208); *Kinney Co.*, 2 mi W Bracketville (TNHC 42218), 5 mi WSW Bracketville (TNHC 47577), 5.9 mi E Bracketville (LSUMZ 32643), 9.9 mi W Bracketville (TCWC 63677), 13.6 mi E Spofford (TCWC 63918), 1.8 mi E & 4 mi S jct Rio Grande & Sycamore Creek (UTACV 7980); *LaSalle Co.*, Cotulla (CU 1760), between Encinal & Atlee on I-35 (TNHC 41907); *Live Oak Co.*, 13 mi SSE Campbellton (TCWC 14796), George West (TNHC 24492), near George West (TNHC 4306), 5 mi N George West (SM 8948), 3 mi W Three Rivers (TCWC 10587), 5 mi SSW Three Rivers (TNHC 25892), 0.3 mi S Whitsett (KU 145894–145895); *Maverick Co.*, Eagle Pass (USNM 1972 holotype), 1 mi W Quemado (UMMZ 113153); *McMullen Co.*, N McMullen Co (UMMZ 74333), 2 mi E San Miguel Creek on Hwy 173 (TNHC 28757), Tilden (CU 612), 25 mi S & 12 mi E Tilden (TNHC 47506), jct Hwys 624 & 16 (TAIC 2046); *Refugio Co.*, 3 mi W Woodsboro (DMNH 3070); *San Patricio Co.*, Aransas Pass (TAIC 3977), 1.5 mi NW Mathis (TNHC 24554), 2 mi N Mathis (TNHC 24567), 2.5 mi SE Mathis (TNHC 20406), 5 mi SW Mathis (TNHC 15301), 7 mi SW Mathis (TNHC 28362), along Nueces Bay (SDNHM 23190–23191), 1 mi S Sinton (FSM 22104), Welder Wildlife Refuge (MVZ 128099, TCWC 65281); *Starr Co.*, 10.4 mi S Agua Nueva (TCWC 63112), Falcon Heights (TCWC 51838), 5 mi W McCook (CAS 103475), 5 mi W Roma (TCWC 63111); *Val Verde Co.*, 2 mi W Del Rio (TNHC 42219), 2.5 mi W Del Rio (TNHC 42220), W Sacatosa Creek at Hwy 85 (CAS 9856); *Webb Co.*, 15 mi NNE Laredo (AMNH 126734), 37.8 mi NW Laredo (TCWC 42361), 4.1 mi W jct Hwys 44 & 83 on 83 (TAIC 733); *Willacy Co.*, 5 mi W Port Mansfield (TAIC 4072); *Zapata Co.*, no locality (TNHC 23182), 1 mi NE Escobas (TCWC 48657), 5.3 mi S Laredo (UMMZ 74067), along Rio Grande (UMMZ 92797), 6 mi N San Ygnacio (TCWC 36388), 8.4 mi NE San Ygnacio (UTACV 10438); *Zavala Co.*, 5.4 mi S & 6.2 mi E LaPryor (TCWC 64997). **MEXICO: COAHUILA:** 3 mi E Muzquiz (KU 38331), 20 mi E Nava (KU 39960), 18.5 mi SE Saltillo (EAL 3377), 3.4 mi S Villa Union (SDNHM 49792). **GUANAJUATO:** Guanajuato (USNM 10240), Hwy 57 at San Luis Potosi state line (TCWC 65903). **HIDALGO:** Ixmiquilpan (AMNH 72422), 77 km N Ixmiquilpan (ANSP 28689), 8.3 mi N Jacala (UMMZ 106396), 12 mi S Jacala (UAZ 27006), 5 km S Venados (SDNHM 58399), 9 km S Zacualpan

(TTU 6800), 11 km S & 1 km W Zacualpan (TTU 6799), 2 mi W Hwy 85 at S entrance to Zimipan (LACM 128447). **MICHOACAN:** 2 mi W Morelia (MVZ 78364), Tacicuaró (FMNH 100296, USNM 111312). **NUEVO LEÓN:** 4 mi W Allende (KU 68117), Aramberri (KU 87748), 10.4 mi W Cerralvo (EAL 3571), 12 km E & 15 km S Galeana (TU 17551–17552), 1 mi E Iturbida (TCWC 30430), 2 mi S Linares (AMNH 69938), 19 km N & 9 km E Matehuala (FWM 7255), 4 mi S Monterrey (TU 17547), 13 mi E Monterrey (MCZ 46321), 25 mi S Monterrey (UIMNH 3836), 24.8 km S Sabinas Hidalgo (TCWC 60760–60763). **QUERÉTERO:** 6.3 mi El Madroño (TCWC 29489), 0.2 mi E Jalpan (TCWC 32928), km 106 on rd from Jalpan to San Juan del Río (MCZ 157827), 1 mi N Peña Blanca (TCWC 45658), 8 km N Querétaro (SDNHM 49502), 6.4 mi NE San Juan del Río (TCWC 38459), 1 mi E San Pablo Jct (TCWC 53061), 1 mi NW Toliman (TCWC 41012). **SAN LUIS POTOSÍ:** Alvarez (MCZ 19024, 19028–19031, 46452), Bledos (LSUMZ 4204), between Charcas & Venado (UMMZ 77245), 7.5 mi N El Valles (AMNH 67160), La Naranja (TU 17562), 8 mi NE Maíz (AMNH 110413), 13 mi E Maíz (AMNH 85246), 35 km W Maíz (UIMNH 17858), 30 mi NW Maíz (MVZ 129331), 10 mi E Matehuala (CM 60004), 20 mi S Matehuala (AMNH 93427), 24 mi S Matehuala (EAL 24), 38 km SW Río Verde (LSUMZ 5396), 8.5 mi SW San Luis Potosí (UMMZ 120221), 12.7 mi SW San Luis Potosí (FWM 8670), 43.4 km E San Luis Potosí (UTACV 12365), 4.5 mi NNW Santo Domingo (EAL 4201). **TAMAULIPAS:** 4 mi E Aldama (UMMZ 101260), 50 mi S Brownsville (USNM 64681), 25 mi N El Limón (UMMZ 102898), 1 mi S Fortuna (UMMZ 110956), 1.3 mi N Gómez Farias (SM 11425), 4.3 km S Gómez Farias (UTACV 16135), 3 mi N Gómez Farias (SM 8947), Juámave (UMMZ 95204), La Joya de Salas (UMMZ 110818), 29 km N Mante (UMMZ 143724), 27 mi N Mante (UIMNH 3831), Matamoros (USNM 1974), 25 mi SW Matamoros (KU 61064), Miquihuana (MCZ 19552–19553), 11.7 km NW Morales (TNHC 28899), 8 km S Nuevo Laredo (UTACV 12364), 0.3 mi SW Rancho Carricitos (TCWC 49933), 12 km SE Reynosa (UMMZ 143723), 20 mi ESE Reynosa (MVZ 36748), Soto La Marina (USNM 37546), Victoria (AMNH 75935), 7 mi N Victoria (MCZ 46322), 15.5 mi SW Victoria (UMMZ 114675), 22 km N Victoria (USNM 111279), 18 mi SW Victoria (AMNH 104465), 63 km E Victoria (TCWC 26730), 3 mi N Villagrán Monterrey (TNHC 32323), 1 mi S jct Hwy 101 & San Carlos rd (FSM 42308). **VERACRUZ:** 9 mi SE Jalapa (UO 33467), 35 mi S Nautla (TAIC 2648).

Masticophis taeniatus × *M. Schotti*.—**UNITED STATES: TEXAS:** *Uvalde Co.*, 13 mi N Uvalde (TCWC 49204); *Val Verde Co.*, 8.5 mi NW Del Río on US 90 (CAS 9864), mouth Pecos River (UMMZ 74334). **MEXICO: COAHUILA:** del Carmen Mtns (FMNH 25301), 14.2 mi N Saltillo (TCWC 54321–54322). **NUEVO LEÓN:** 20 mi SSW Galeana (FWM 7931), 5 mi E San Roberto (ANSP 28688).

Masticophis bilineatus.—**UNITED STATES: ARIZONA:** no locality, (ANSP 5362); *County unknown*, Colorado Bottom (USNM 1981); *Cochise Co.*, Bisbee (BYU 256), 25 mi W Bisbee (CA 7809), 30 mi W Bisbee (CA 7470), 6 mi SSW Carr Canyon (AMNH 84969), Chiricahua Mtns (AMNH 75361, CU 10679, LSUMZ 8799, MVZ 7943, 8193, 44932, 97078, TCWC 63048, UMMZ 114130, UTEP 2824, 9592), 1 mi N Dox Cabezas (MVZ 6942), 15 mi S Ft Huachuca (UIMNH 6062), Huachuca Mtns (ANSP 16488, BYU 30029, 31880, MCZ 11409, MVZ 5406, 44742), Portal (AMNH 80816, 91620–91621, 109438–109439), 0.5 mi E Portal (CU 10660), 0.4 mi S & 0.8 mi W Portal (AMNH 11159), 1 mi SW Portal (AMNH 84972, 99333, CM 66092), 1.5 mi E Portal (MVZ 137578), 2 mi W Portal (CA 5070), 2 mi S Portal (CM 66057), 2 mi E Portal (LACM 2257), 3 mi W Portal (AMNH 91622), 3.5 mi SW Portal (ASC 6597), 4 mi NW Portal (UMMZ 121839, 121917), 5 mi W Portal (UMMZ 114633), Southwestern Research Station–SWRS (AMNH 80817, 84971, 111193–111194, 123866, FSM 8690, LACM 2255, MVZ 67188, 67204), 0.25 mi W SWRS (AMNH 84970), 2.5 mi W SWRS (LACM 133880), 3.4 mi S Silverspur (UIMNH 72001), Tombstone (CU 2320), 20 mi W Willcox (CA 16456); *Gila Co.*, no locality (USL 18840), 2 mi NW Coolidge Dam (UMMZ 114634), 20 mi N Globe (TNHC 16793), Roosevelt Lake (USL 8408), 8 mi S Salt River (ASU 1716), 10 mi N Salt River on Hwy 60 (CA 9520), Salt River Canyon (ASU 10536–10538), Sierra Ancha Experimental Forest (CM 51907–51908); *Graham Co.*, 5 mi SE Bonita (ASU 7030), Camp Grant (USNM 8434), 0.25 mi S Cyclone (UIMNH 24555), Gila River Sec 28 T6S R28E (CM 70672), Marijilda Base Camp (ASU 7020, 7032–7033), 3 mi E Marijilda Base Camp (ASU 7014), Marijilda Canyon (ASU 7770, CM 48661, 51492, 70891, 70900, 70933, 70944), Pinaleno Mtns (CA 17006, CM 69819, 71041, 71067, 71254, 71537, 71629, 71667, 107289), 11 mi SW Safford (CA 11083), 11 mi S & 4.5 mi W Safford (ASU 7011, 7017), 25 mi W Safford (CA 12974), 30 NW Safford (UIMNH 71999–72000), Mt Turnbull (USNM 54719), 5.4 mi SW jct Hwys 366 & 666 on 366 (UTEP 9545); *Greenlee Co.*, Eagle Creek (CM 71184, 70746), Gila River (CM 71425); *Maricopa Co.*, 10–20 mi N Ajo (ASU 13846), 11 mi N Apache jct (CM 48620), Ashdale Ranger Station (USL 6724), 7.8 mi ENE Carefree (CM 69160), Cave Creek (ASU 753), E of Mesa (ASU 59), Morristown (SDNHM 8414), 4.8 mi N Morristown (CA 16158), 1 mi N Sunflower (ASU 3686), Tortilla Flats (ASU 9085, CAS 80670), 5.5 mi SE Wickenburg (UIMNH 71996–71997), 7 mi SE Wickenburg (UIMNH 71998); *Mohave Co.*, 15

km W Bagdad (ASU 14488), Hwy 93 at mile post 157.7 (ASU 22134); *Pima Co.*, 0.5 mi S Ajo (UAZ 36767), 2 mi W Ajo (UAZ 40028), 24 mi S Ajo (NMSU 2634), Kitt Pk Observatory (UAZ 25158), 1.3 mi E jct Hwy 86 & Kitt Pk Rd on 86 (UAZ 32787), 2.8 mi from Hwy 86 & Kitt Pk Rd on 86 (UAZ 20794), 3.2 mi E jct Hwy 86 & Kitt Pk Rd on 86 (UAZ 20756), 3.6 mi from jct Hwy 86 & Kitt Pk Rd on 86 (UAZ 20796), 4.1 mi E jct Hwy 86 & Kitt Pk Rd (UAZ 20795), 7.3 mi from jct Hwy 86 & Kitt Pk Rd on 86 (UAZ 20786), 3.7 mi below jct Kitt Pk Rd & Picnic Area Rd (UAZ 20783), Organ Pipe Cactus National Monument (CM 48524, UIMNH 5611), 0.5 mi from Pima Canyon mouth (TCWC 30720), 22.9 mi W Robles Jct (UAZ 20799), Sabino Canyon Rec Area (INHS 7571, 8007), Santa Rita Mtns (MU 2494), Sells (FSM 56664), 8 mi N Sonoita (UAZ 36250), 8.7 mi N Sonoita (UAZ 20765), 15.2 mi N Sonoita (UAZ 34699), 8 mi N Tanque Verde Rd on Mt Lemon Rd (MVZ 180258), 14 mi N Tucson (CA 3929), 50 mi S Tucson (EAL 883); *Pinal Co.*, 30 mi S Phoenix (CA 16157), Picket Post Mtns (CA 9825), Superior (ASU 1622, CA 9525, 9680), 5 mi W Superior (CA 13579–13580), 6 mi E Winkelman (UIMNH 37712); *Santa Cruz Co.*, 7.7 mi W Ft Huachuca (UTEP 11162), 8.9 mi WNW Lochiel (LSUMZ 40983), Patagonia (CU 5234), 3 mi S Patagonia (CU 5492), 2 mi SE Ruby (LSUMZ 32900), 8.8 mi W jct Hwys 89 & 289 (EAL 2770), 9.8 mi S Jct Hwys 82 & 83 on 83 (TCWC 63379); *Yavapai Co.*, Bradshaw Mtns (AMNH 63977), 2.2 mi NE Hillside (BYU 37042). **NEW MEXICO:** *Hidalgo Co.*, Adobe Creek center Sec 24 T31S R19W (AMNH 77453), Animas Mtns (AMNH 84976, 87276, UNM 6979), 8 mi W Animas (AMNH 84974–84975), 8.5 mi S & 2 mi W Animas (NMSU 6395), 3.5 mi W Cloverdale (UNM 8298), 7.5 mi NW Cloverdale (LACM 2253), 10.5 mi N & 13.5 mi E Cloverdale (UTEP 1344), 16 mi NE Cloverdale (CM 18222), Guadalupe Mtns (UNM 3334, 6786, 8297), Indian Creek Canyon (UNM 13820), Peloncillo Mtns (AMNH 75949–75950, 119512, UNM 7687), 7 mi S Rodeo (MVZ 67203), 8 mi SSE Rodeo (CU 5768), 17 mi N & 3 mi E Rodeo (UNM 39100), San Geronimo Trail 5 mi E AZ state line (LACM 2254), 2 mi SW Steins (LSUMZ 8806), 8.2 mi S jct Hwys I-10 & 80 on 80 (LACM 76563), SW 0.25 Sec 15 T34S R21W (UNM 32349). **MEXICO:** **AGUASCALIENTES:** 2 km W Calvillo (UTEP 7747), 4.5 mi E Calvillo (LSUMZ 35033). **CHIHUAHUA:** near Batopilas (USNM 46382). **COLIMA:** no locality (MCZ 11409), Colima (AMNH 19636). **DURANGO:** Santa Ana (KU 74567), 2 km E Villa Corona (UTEP 3977). **JALISCO:** 2 mi E Bolanos (KU 91424), 10.1 km SW Cocula (TCWC 48059), Guadalajara (USNM 32212), 4.8 km S Huejucar (KU 102966), Hwy 15 S of Lago de Chapala (TCWC 33793), 5.3 mi S Nayarit state line near Ixtlan del Rio (UIMNH 40361), 13 mi N Sayula (AMNH 93339), 4.8 km E Totatiche (KU 100512), 10 mi NE Union de Tula (MVZ 7220). **NAYARIT:** 17.9 mi SW Acaponeta (FSM 24761), 11.4 mi S Acaponeta turnoff (LACM 6990), Jesus Maria (AMNH 74953–74956), between Marquezado & Auzata (AMNH 19640), 15 mi E San Blas (UIMNH 71988), Hwy 15 near Sinaloa border (LACM 6989), 2.4 mi N Tecuala turnoff (UIMNH 85728), Tepic (USNM 46417), rd from Tepic to Paga (LACM 8739). **OAXACA:** Cuicatlam (USNM 46499). **SINALOA:** 4 mi S Casa Blanca (KU 83406), 0.2 mi W Concordia (LACM 6992), 10 mi W Concordia (UMMZ 102483), 15.6 mi N Culiacan (UIMNH 71992), 37.5 mi N Culiacan (UIMNH 71991), 72 mi S Culiacan (FSM 42096), Elota (UIMNH 83457), 12 mi N Escuinapa (UIMNH 41593), 17.2 mi NW Escuinapa (TNHC 25475), 30 mi S Escuinapa (UIMNH 71994), Isla Palmito del Verde (KU 73569–73570), 15 mi N Los Mochis (CM 54004), Mazatlán (TCWC 21903), 1.1 mi N Mazatlán (UIMNH 83456), 15.8 mi N Mazatlán (LACM 103106), 26.8 mi N Mazatlán (LACM 103104), 29 mi N Mazatlán (UIMNH 71989), 52.4 mi N Mazatlán (UIMNH 71900), Hwy 15 5 mi N Nayarit state line (LACM 6991), Rosario (KU 73568), San Ignacio (LACM 6986), Terreros (LACM 6993), 8 km N Villa Union (KU 80757), 5.8 mi NW Villa Union (CAS 24114), 18 mi SW Villa Union (CAS 120883), 34 mi NE Villa Union (LACM 103105), 6.2 mi N & 10.6 mi E jct Hwys 40 & 15 (CAS 23954–23955). **SONORA:** no locality (ASU 8421), 47 km E Agua Prieta (UTACV 17796), Alamos (MCZ 43251), W of Alamos (CAS 140518), 1 mi W Alamos (LACM 103109), 2 mi SSE Alamos (LACM 103107), 4 mi W Alamos (LACM 103108), 7 mi W Alamos (ASU 6037–6038, 6454, 6645), 17 mi W Alamos (ASU 6510), 17 mi S Casa Blanca (MVZ 67430), 0.4 mi NE El Coyote (MVZ 136780), S El Novillo 9MVZ 136781), Guaymas (MTKD 15068 paratype, 15523 holotype, USNM 15880), 4 mi SW Guaymas (KU 48919–48920), Guirocoba (AMNH 63722–63723, MVZ 50793–50796), 5 mi S Hermosillo (UMMZ 72103), 5 mi SW Hermosillo 9FMNH 102669), 32 mi SE Hermosillo (AMNH 84978), Isla San Esteban (KU 91587, LACM 20601–20604, 74047, MVZ 74954–74956, 76499, SDNHM 3826, 40855, TTU 8017, UMMZ 128928), Isla San Pedro Martir (UO 32528), Isla Tiburon (USNM 222054–222058), 5 mi SE La Pintada (AMNH 80815), La Posa (FMNH 102670, UIMNH 17838), Las Chispas (AMNH 3469), 25 mi W Maxatan (AMNH 84977), San Luis Mtns (USNM 21053–21054, UTACV 17794–17795), 4.5 mi S Tubutama (CAS 16642), 5 mi S Tubutama (CAS 17297), between Vicam & Guaymas (LACM 103110). **ZACATECAS:** 9 mi SSW Jalpa (UTEP 7748), 1.7 mi N Los Bajios (LSUMZ 26233), San Juan Capistrano (USNM 46481), 7 km S Santa Rosa (UTEP 3978), Zapogui (USL 12283).

APPENDIX 2

Electrophoresis Samples

Masticophis bilineatus.—**ARIZONA:** Cochise Co. (TCWC 63696); Pima Co. (TCWC 64995). **NEW MEXICO:** Hidalgo Co. (TCWC 64842).

Masticophis s. schotti.—**TEXAS:** Frio Co. (TCWC 63774, 63919); Jim Wells Co. (TCWC 64839); San Patricio Co. (TCWC 65281); Zavala Co. (TCWC 64997).

M. s. ruthveni.—**TEXAS:** Cameron Co. (TCWC 65282); Hidalgo Co. (TCWC 65283). **MEXICO:** GUANAJUATO: (TCWC 65903).

Masticophis t. taeniatus.—**IDAHO:** Ada Co. (TCWC 64836–64837). **NEW MEXICO:** Catron Co. (TCWC 65001); Hidalgo Co. (UTEP 11355); Sierra Co. (NMSU uncatalogued); Socorro Co. (TCWC 66165).

M. t. girardi.—**TEXAS:** Brewster Co. (TCWC 64999, 65285); Edwards Co. (TCWC 65923); El Paso Co. (TCWC 64998, UTEP 10804); Kimble Co. (TCWC 64809, 65284, 65287); Llano Co. (TCWC 63772–63773, 63876, 64841, 64996, 65000); McCulloch Co. (TCWC 64838); Medina Co. (TCWC 63775); Presidio Co. (TCWC 64810–64811, 65286); Uvalde Co. (TCWC 64840).

U-SHAPED ORIENTATION OF HUNTER-SCHREGER BANDS IN THE ENAMEL OF *MOROPUS* (MAMMALIA: CHALICOTHERIIDAE) IN COMPARISON TO SOME OTHER PERISSODACTYLA

WIGHART V. KOENIGSWALD¹

ABSTRACT

In the Chalicotheriidae the main shearing facets of upper and lower molars possess a very significant modification of the direction of Hunter-Schreger bands (HSB). In contrast to the primitive horizontal HSB orientation, chalicotheres show distinctly U-shaped HSB that intersect the main cutting edges at almost right angles. This relationship is maintained throughout the various stages of wear. This specific characteristic is shared with Brontotheriidae. Certain other Perissodactyla, such as Tapiroidea and Rhinocerotidae, but definitely not the Equoidea, follow a similar tendency. Functionally, the reorientation of the HSB is interpreted as an adaptation to reduce abrasion. The reorientation of the HSB seems to be related to interprismatic matrix (IPM) parallel to the prisms.

ZUSAMMENFASSUNG

Bei den Chalicotheriidae zeigen die Hauptschneidekanten der oberen und unteren Molaren eine auffallende Abweichung von der normalerweise horizontalen Orientierung der Hunter-Schreger-Bänder (HSB). Die HSB sind U-förmig gebogen und stehen annähernd senkrecht auf den Hauptschneidekanten. Dieser Winkel bleibt durch diese spezielle Anordnung auch während der fortschreitenden Abkautung erhalten. Dieses abgeleitete Merkmal teilen die Chalicotheriidae mit den Brontotheriidae. Andere Perissodactyla, wie die Tapiroidea und Rhinocerotidae, nicht aber die Equoidea, verfolgen eine ähnliche Strategie. Funktionell wird diese Reorientierung der HSB als Anpassung gedeutet, durch die der Abrieb der Schneidekante reduziert wird. Die Reorientierung der HSB scheint an eine Interprismatische Matrix (IPM) gebunden sein, die parallel zu den Prismen liegt.

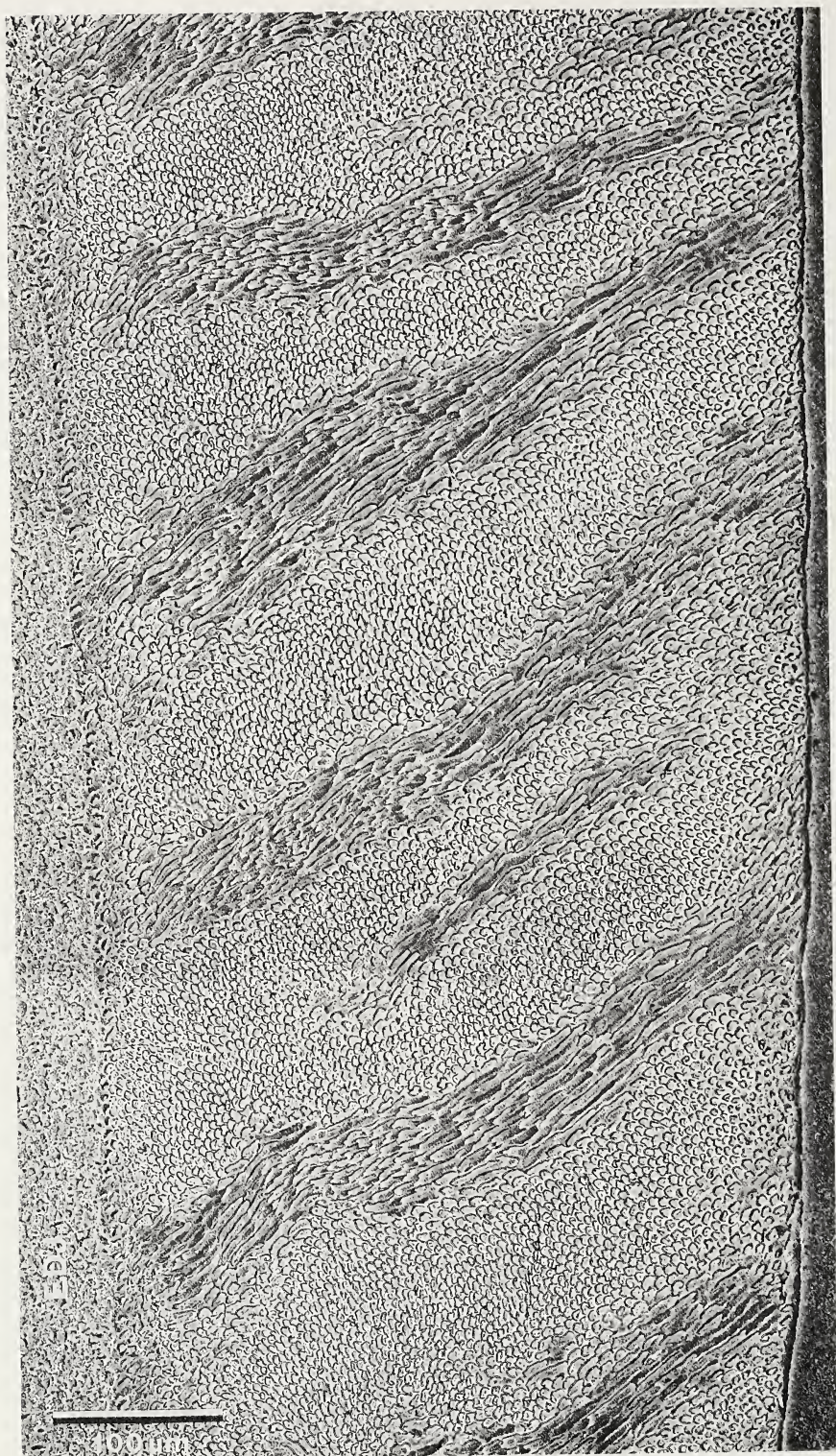
INTRODUCTION

The prismatic enamel of most large mammals is characterized by Hunter-Schreger bands (HSB). These are light and dark bands often visible in low-powered light microscopy. The SEM shows their nature as decussating layers of enamel prisms (Fig. 1). The most common orientation of these bands is roughly parallel to the alveolar surface of the jaw, which is here termed the "horizontal orientation."

In contrast to most other large mammals, several groups of perissodactyls such as Chalicotheriidae, Brontotheriidae, Tapiroidea, and Rhinocerotidae (but not Equoidea) modified the horizontal orientation of HSB. The vertical orientation of HSB in Rhinocerotidae was described by Rensberger and Koenigswald (1980) and Boyde and Fortelius (1986). Rensberger and Koenigswald (1980) interpreted the modified orientations found in Tapiroidea and Brontotheriidae as structural intermediates in the evolution toward Rhinocerotidae.

This paper describes the modified orientation of HSB in the schmelzmuster of Chalicotheriidae. The study is based on various jaws (including milk dentitions) of *Moropus elatus* and *Moropus* sp. from the Agate Springs Quarries, lower Harrison Formation, Nebraska (Holland and Peterson, 1914). The extremely well-

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preserved enamel and the specific schmelzmuster allows a tracing of the orientation of the HSB over almost the entire surface of the teeth. The material was generously made available by the Carnegie Museum of Natural History.

The schmelzmuster of *Moropus* is compared with that of other Chalicotheriidae, Brontotheriidae, and other Perissodactyla. This survey allows a discussion of functional aspects of the orientation of HSB.

HUNTER-SCHREGER BANDS

Hunter-Schreger bands (HSB) constitute one of the basic enamel types (Koenigswald, 1980, 1982) widely distributed among mammals. This enamel type is characterized by layers of enamel prisms of regularly alternating direction. Prisms of adjacent layers often decussate at a high angle of up to 90°. The thickness of the bands counted in prism diameters is significant for rodent incisors (pauciserial, multiserial, or uniserial) (Korvenkontio, 1934; Wahlert, 1968), but shows a wide individual variation in larger mammals (Fig. 1). Average thickness between 5 and 20 prisms have been counted by Kawai (1955) for various species. Mostly commonly, thickness tends to be around ten prisms. But thickness is only one of the characters of the HSB. The bands share regular bifurcation patterns as shown in Fig. 5C, 6C, and prisms change over from one band to the next in the transitional zones between bands (Koenigswald and Pfretzschner, 1987). As seen in cross sections through the enamel, HSB often form only one layer of a given schmelzmuster and are combined with an inner and/or outer layer of radial enamel, a different enamel type in which the prisms do not decussate.

As planar elements, the HSB show two distinct directions (Fig. 2). The one observable in the vertical cross section between the enamel-dentine junction (EDJ) and the outer surface is defined as inclination (Korvenkontio, 1934). The inclination is 0° when the bands are perpendicular to the EDJ. The second direction is the lateral orientation which can be studied on the translucent enamel surface or in tangential sections through the layer with HSB. Based on commonality among Mammalia, the least derived lateral orientation is horizontal—that is, parallel to the alveolar margin of the jaws. This paper concentrates on modifications of the lateral orientation of HSB.

METHODS

Enamel prisms function like optic fibers when exposed to a strong source of light. The individual prisms are too thin to be observed under a low-powered microscope, but since all prisms within one band have the same orientation, their optic activity sums up, and HSB become visible even at low magnification. When the enamel is illuminated parallel to the bands, they become visible as light and dark areas. The prisms of all dark areas point toward the light source, whereas the prisms in light areas form a larger angle with the direction of the light (Koenigswald and Pfretzschner, 1987). By handling the tooth in front of a strong light source like fiber optics under a binocular microscope, the lateral orientation of the HSB can be studied at 20 to 50 times magnification. At the same time, the

Fig. 1.—*Moropus* sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene. Scanning electron micrograph of longitudinal section through the protoconid of the lower molar, depicting Hunter-Schreger bands of varying thickness. (EDJ = enamel dentine junction.)

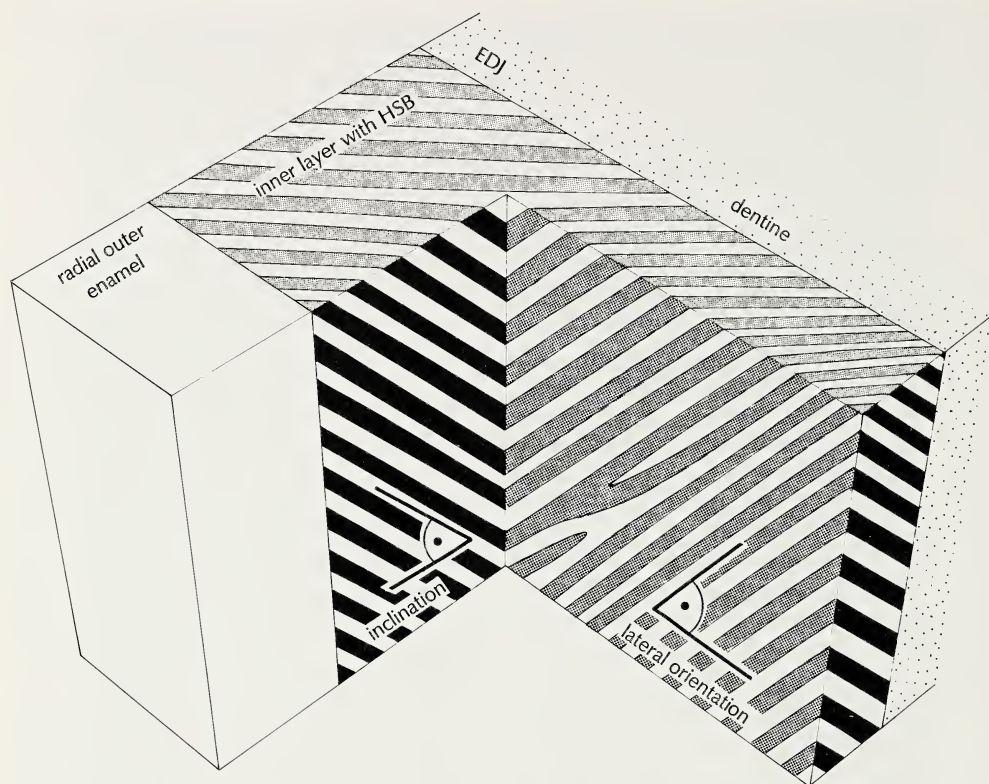


Fig. 2.—Diagram to illustrate inclination and lateral orientation of Hunter-Schreger bands (HSB). Inclination is defined as the angle between the HSB and a plane parallel to the enamel dentine junction (EDJ). It is seen best in a vertical cross section. Lateral orientation is usually horizontal but in some cases, as in chalicotheres, rotated. The HSB include an angle with the plane parallel to the alveolar margin of the jaw. In the enamel depicted here, two layers of different enamel types form the schmelzmuster, as in chalicotheres or brontotheres, having an inner layer with HSB and an outer layer with radial enamel.

unilateral bifurcation of the bands then becomes visible (Koenigswald and Pfretzschner, 1987).

In order to facilitate the mapping of these observations, casts were made from the teeth studied and the directions of the HSB were drawn on the plaster casts as observed.

A thick layer of outer radial enamel or a structured enamel surface can often obscure the visibility of the HSB. Pericymata on the enamel surface, although occasionally parallelling the HSB, must not be mistaken for HSB, since they are fundamentally independent structures.

To study the schmelzmuster and the orientation of the HSB from sections of teeth or tooth fragments, they have to be embedded into epoxy resin, sectioned, and ground in the desired direction. On a tangential section through the layer containing HSB, the lateral orientation of the HSB can be studied even when they are not visible from the outside. The prisms show the same optical properties in sections as in surface views. These properties become even more visible when etched (e.g., with 2N HCl for 2–5 sec). The etched surfaces, coated with a con-

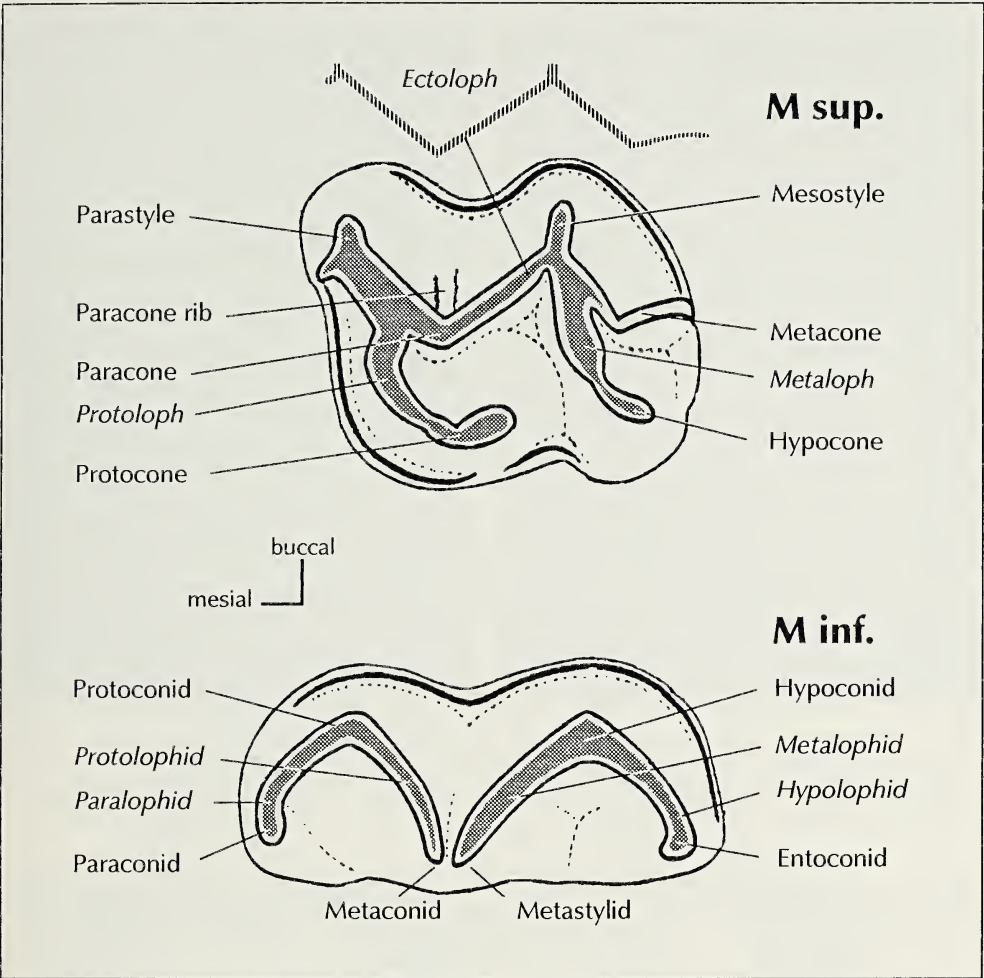


Fig. 3.—*Moropus* sp. Tooth cusps in upper and lower molars. Modified after Coombs (1978) and Thenius (1989).

ducting element (e.g., gold palladium), can be studied for further details of the complex enamel structure under the SEM.

Morphological terms used for the description of *Moropus* (Fig. 3) follow Thenius (1989) and Coombs (1978).

SCHMELZMUSTER OF *MOROPUS*

The schmelzmuster of *Moropus* is characterized by HSB that continue from the EDJ almost to the outer surface (Fig. 1). The angle of decussation is reduced in an outer zone which continues into a thin radial enamel. The inclination of the HSB is slight and concave upwards. In a tangential view of the HSB are slightly wavy and bifurcate frequently. The lateral orientation of the HSB varies: it is horizontal at the base of the crown but strongly bent to intersect the main cutting edges almost vertically. A detailed description is given below. The prisms generally

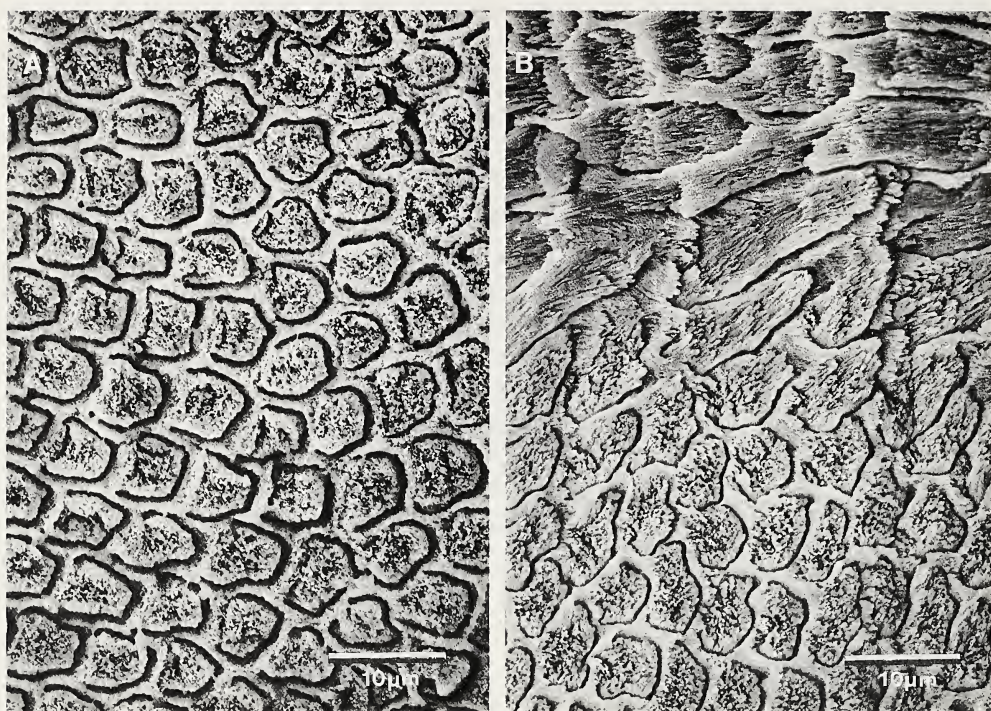


Fig. 4.—*Moropus* sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene. A: SEM micrograph of enamel prism cross sections in a tangential ground and etched section of the lower molar. Most prisms have an open but somewhat irregular prism sheath. B: Prisms in cross section and longitudinal aspect at the border between HSB. The IPM is almost parallel to the prisms.

have an incomplete prism sheath (Fig. 4A). The cross section is rounded or angular. Prisms show a “seam” (Lester and Koenigswald, 1989), especially near the EDJ. The IPM crystallites run almost parallel to the prisms and surround them.

ORIENTATION OF HUNTER-SCHREGER BANDS

Upper molar morphology is characterized by a single series of shearing facets which is formed by the ectoloph (Fig. 3). While parastyle and mesostyle remain almost vertical, the paracone and metacone are strongly inclined, which results in a strong flexion of the ectoloph. The enamel on the buccal side is much thicker than on the lingual side. The protocone and the hypocone are on the lingual side. The hypocone forms a second shearing facet positioned lingually from the metacone. The protocone is only slightly linked to the ectoloph by the protoloph and forms an almost isolated rounded cusp.

In the upper molars the HSB are oriented horizontally in the cingulum and at the base of the crown. The horizontal orientation of the HSB is retained on the lingual side of the hypocone and on all sides of the protocone to its full height. On the buccal side of the ectoloph, however, the lateral orientation of the HSB is strongly modified as follows. Parastyle and mesostyle retain the horizontal HSB, but on the prominent paracone the ectoloph forms two cutting edges that enclose an angle of roughly 90°. HSB are bent in a U-shaped fashion to intersect the cutting edges at an almost right angle (Fig. 5A, C). Below the tip of the paracone

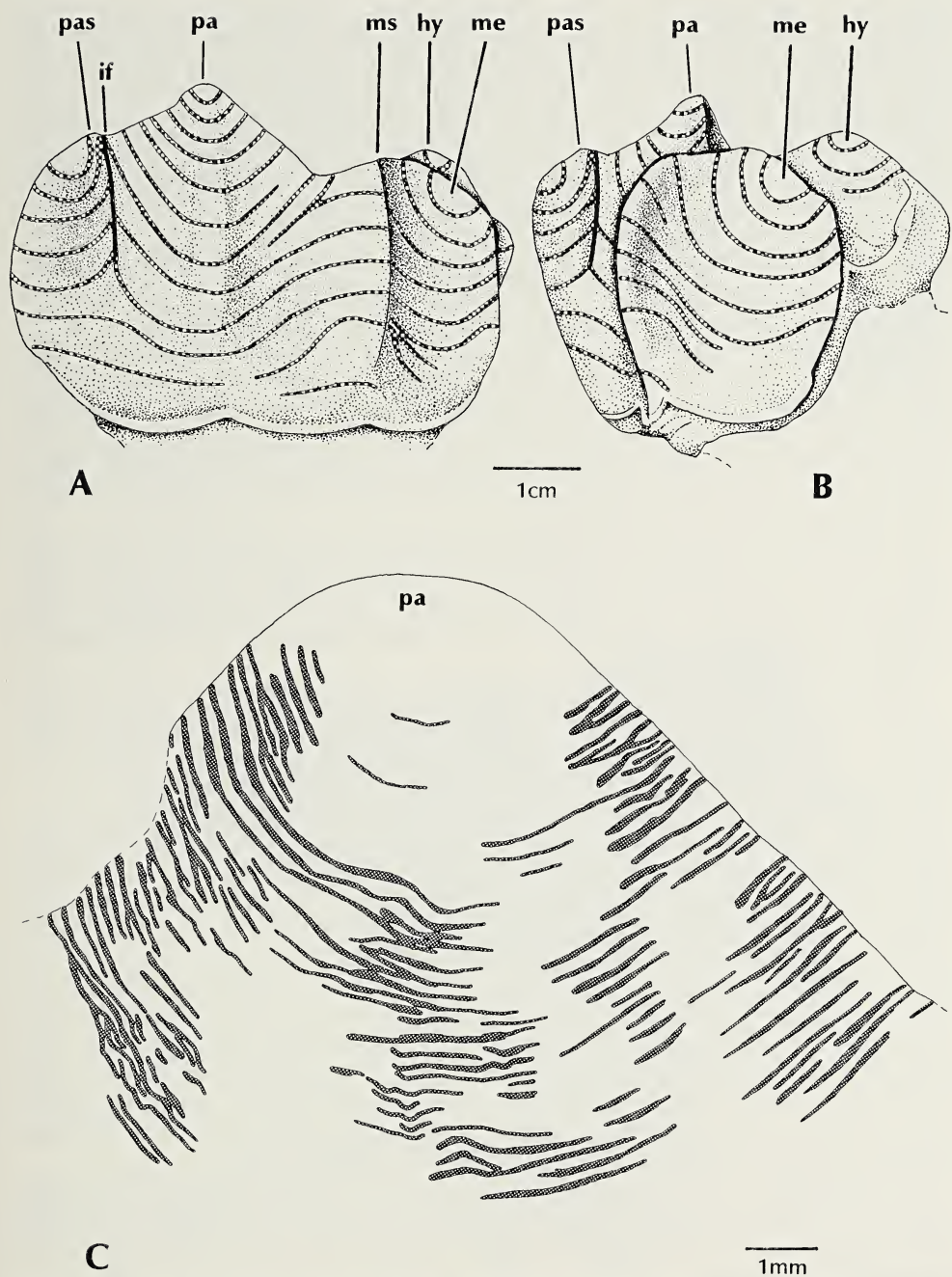


Fig. 5.—*Moropus* sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene. Upper M³. A: diagrammatic HSB orientation in the ectoloph between parastyle and mesostyle. B: diagrammatic HSB orientation in the ectoloph between mesostyle and metastyle. C: detailed mapping of the U-shaped HSB orientation in the paracone (detail from A). Abbreviations: if, interface between fields of HSB; hy, hypocone; me, metacone; ms, mesostyle; pa, paracone, pas, parastyle.

the HSB pass through a short horizontal section. If the paracone rib is prominent, the HSB may even be flexed downward forming an acute angle. Between the horizontal HSB related to the paracone and the inclined HSB related to the parastyle, there is a distinct interface in which the HSB of both dental elements meet at an acute angle. This interface is marked by a slight crease in the enamel surface. But between paracone and mesostyle the fields of HSB grade into each other without a distinct border. Since HSB bifurcate frequently, such a transition from strongly inclined to horizontal HSB is made possible.

In the distal part of the ectoloph the metacone is not morphologically distinct. However, the orientation of the HSB clearly indicates the position of this cusp within the ectoloph. On the metacone the HSB orientation is similar to that of the paracone. Whereas HSB are steeply oriented on both flanks they pass through a narrow horizontal stretch below the cusp. Because of the U-shape, the HSB are again oriented almost normal to the cutting edge between metacone and mesostyle. On the other flank of the metacone they intersect the descending ectoloph at a high angle. The hypocone, which is linked to the ectoloph by the metaloph, shows a U-shaped orientation of the HSB on the buccal side. On the lingual side HSB orientation is more or less horizontal.

The upper milk dentition is generally molariform and follows the same basic pattern. In the premolars the protocone is relatively bigger and somewhat buccolingually compressed, thus forming a short cutting edge comparable to the ectoloph. The HSB are slightly flexed and therefore approach the cutting edges at almost right angles as well.

In the lower molars trigonid and talonid form similar triangles which are connected at the twin cones of metaconid and metastylid. The W-shaped buccal side forms the shearing facets working against the ectoloph of the upper molars. The enamel is again thicker on the buccal side than on the lingual side.

The W-shaped cutting edge is formed by the paralophid, protolophid, metalophid, and hypolophid (Fig. 3). The base of the crown and the lingual sides of the main cusps show distinct horizontally-oriented HSB (Fig. 6A). In a protoconid and hypoconid the HSB are similarly U-shaped as in the ectoloph of the upper molars. While the HSB pass through a narrow section of the horizontal orientation and the buccal side of the protoconid and hypoconid, they bend upward toward the cutting edges on both flanks of each cone (Fig. 6A). Distinct interfaces are found between the cusps situated more to the lingual side. The interfaces are best seen in the paralophid and hypolophid separating the field of HSB related to the paraconid and protoconid and the entoconid and hypoconid, respectively (Fig. 6B, C). Distinct interfaces separate the HSB fields of the twin cusp metaconid/metastylid from that of the protoconid and hypoconid. These interfaces converge onto the central valley and do not reach the base of the crown.

The molariform P_4 and the milk teeth follow a similar pattern as far as they could be investigated. In the anterior premolars (P_2 and P_3) the HSB are slightly flexed towards the shearing facets. In the incisors of the lower jaw HSB are all horizontally oriented.

The pattern described above was found in all available teeth of *Moropus elatus* and *Moropus* sp. as well as in the European *Chalicotherium goldfussi* and the Asian *Chalicotherium* cf. *habeneri*. The congruence of this character in several related genera excludes the possibility that the U-shaped HSB orientation is an individual variation and implies that it is characteristic of the Chalicotheriidae in general. Individual variation within the group occurs on a much smaller scale, and concerns the thickness, bifurcation, and exact orientation of HSB.

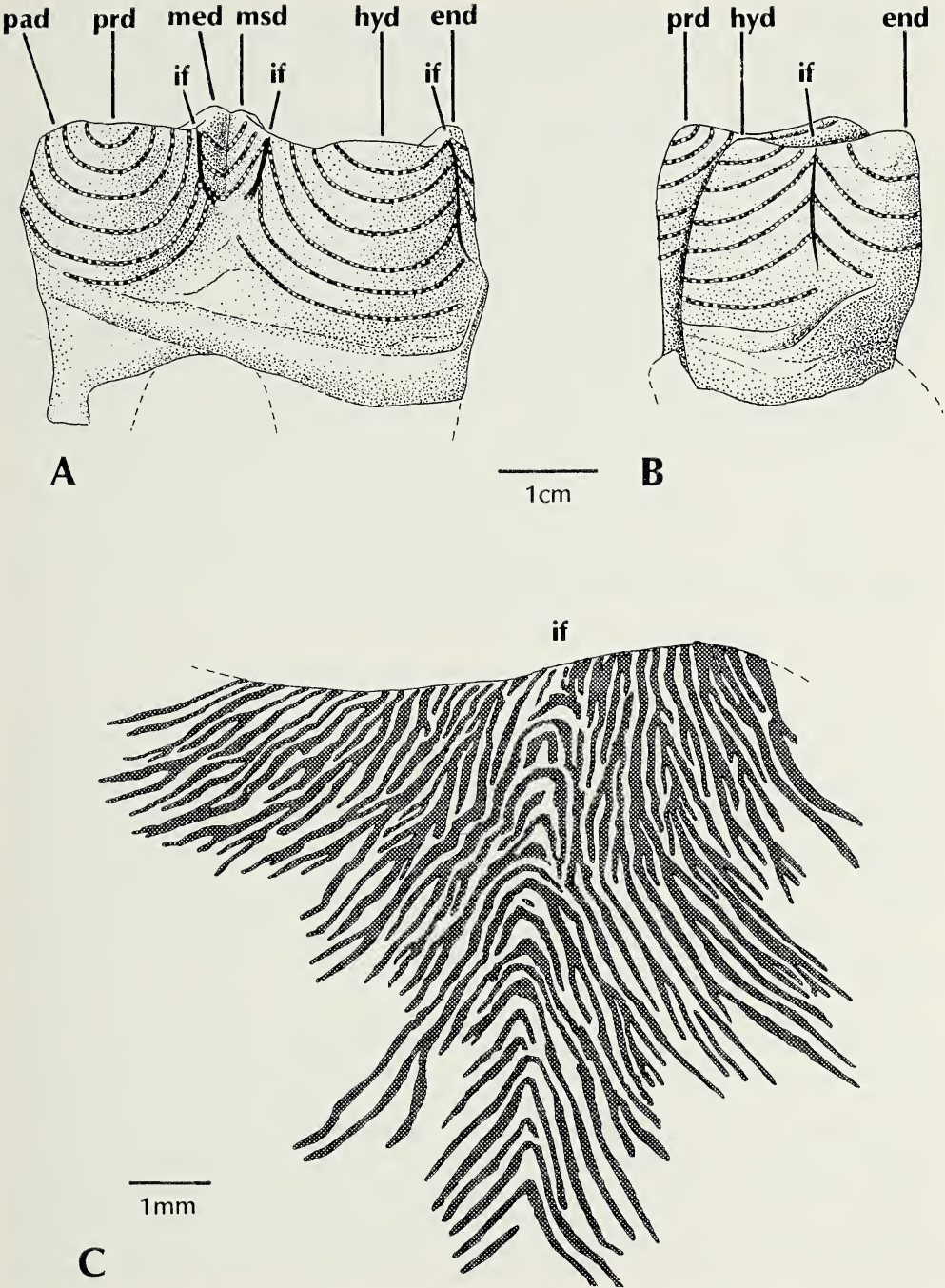


Fig. 6.—*Moropus* sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene. Lower M₁. A: diagrammatic HSB orientation on the buccal side. B: schematic HSB orientation on the hypolophid with interface. C: detailed mapping of the HSB orientation in the hypolophid with an interface between areas of the hypoconid and entoconid. Abbreviations: end, entoconid; if, interface between fields of HSB; hyd, hypoconid; med, metaconid; msd, metastylid; pad, paraconid; prd, protoconid.

ORIENTATION OF THE HSB IN OTHER PERISSODACTYLS

Equoidea

In the well-documented evolution of the Equidae, the HSB consistently retain a horizontal orientation. The basic schmelzmuster, as in *Hyracotherium*, shows horizontal HSB penetrating from the EDJ almost to the outer surface where a thin radial enamel is found. The crystallites of the IPM run parallel to the prisms (Pfretzschner, 1993, in press). In *Mesohippus* and *Anchitherium* this basic schmelzmuster is retained, but the IPM crystallites form an angle with prisms and are arranged in inter-row sheets.

When the molars of Equidae become hypsodont as in *Merychippus*, *Hipparion*, or *Equus*, the schmelzmuster is reorganized. A layer of "modified radial enamel" characterized by thick, vertical inter-row sheets is introduced between the EDJ and the layer of HSB (Pfretzschner, 1993, in press; Koenigswald et al., 1993). Nevertheless, the horizontal orientation of the HSB is retained unchanged.

Palaeotherium sp. (Palaeotheriidae) shows well-developed HSB (Remy, 1976) which are generally oriented horizontally. Although the paracone and metacone in the ectoloph of the upper molars are similarly inclined and shaped as in *Moropus*, the HSB retain their horizontal orientation (Fig. 7A). This documents that HSB orientation is independent of the shape of the ectoloph.

Brontotheriidae

In comparison to the Chalicotheriidae studied, the enamel in the larger Brontotheriidae, such as *Menodus proutii*, is fairly thick. The schmelzmuster of Brontotheriidae is in most cases two-layered. An inner layer is formed by HSB which are only very slightly inclined toward the occlusal surface concave up. The thickness of HSB with an oblique lateral orientation is difficult to quantify since the likelihood of finding these bands at an angle other than 90° is very high. The thickness counts therefore are commonly too high. The HSB disappear in the outer layer of radial enamel. This outer layer is almost as thick as the inner layer and prevents observation of the HSB from the outer surface of the enamel.

The prisms of the radial enamel rise apically at a maximum of about 45°. The prisms have incomplete prism sheaths and the IPM is mainly parallel to the prisms.

In areas with thin enamel, the outer radial enamel may be reduced in thickness or missing. On the occlusal surface, however, the outer radial enamel on the outside is worn off more rapidly than the inner layer of HSB. Therefore, the direction of the HSB can be observed near the occlusal surface. In the angled ectoloph of the upper molars, a U-shaped orientation is found at the paracone and the metacone as described for *Moropus*. In lower molars a similar U-shaped orientation of the HSB is found at the hypoconid and the protoconid just as in *Moropus*. In the paralophid, protolophid, metalophid, and hypolophid, interfaces with very sharp turns of the HSB are present as described for the Chalicotheriidae. These interfaces are visible at the occlusal surface but can be observed better in a tangential ground section.

Tapiroidea

The schmelzmuster of *Tapirus* (Tapiridae) is characterized by horizontal HSB which extend to the outer surface. The prisms show an open prism sheath and

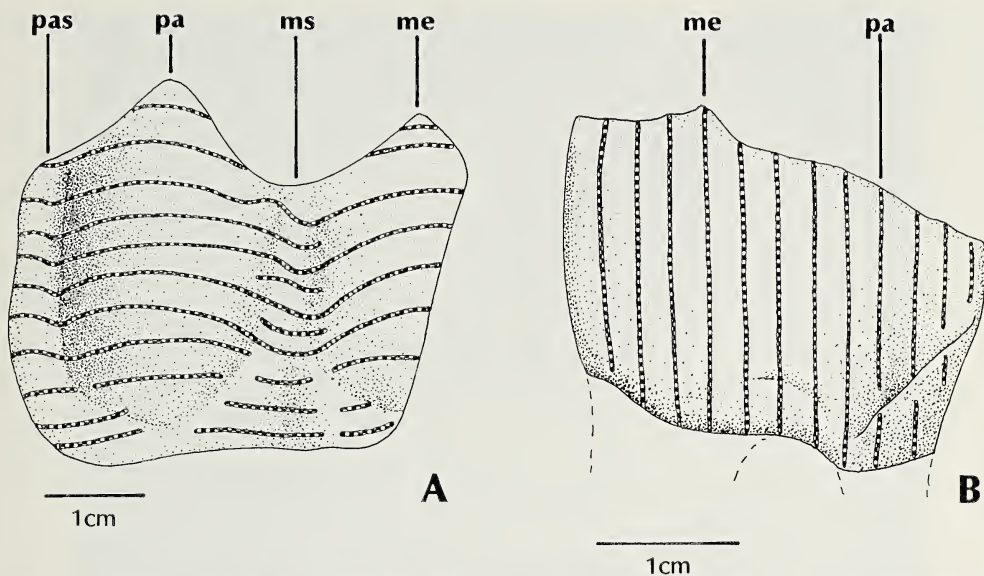


Fig. 7.—Hunter-Schreger band orientation in Equoidea and Rhinocerotidae. A: *Palaeotherium* sp. (Equoidea) Frohnstetten, Germany, lower Oligocene. Diagrammatic illustration of the horizontal HSB orientation in the ectoloph of an upper molar. B: *Floridaceras whitei* (Rhinocerotidae). Diagrammatic illustration of the vertical HSB in the ectoloph of an upper molar. Abbreviations: me, metacone; ms, mesostyle; pa, paracone; pas, parastyle.

are surrounded by IPM, the crystallites of which are almost parallel to the prisms. HSB orientation is modified in *Tapirus* which was discussed for lower molars by Rensberger and Koenigswald (1980). In the lower molars, the HSB of the lingual and buccal sides of the main cusps are horizontal. In the transverse lophs, the HSB bend into an almost vertical direction. In the middle lophs, the fields of HSB of the two involved cusps meet at a distinct interface which often can be seen in the worn occlusal surface as the angle between HSB (Fortelius, 1984: fig. 2b) or on the unworn surface as a slight groove (Fig. 8).

In the upper molars, the horizontal HSB dominate. Only in the uppermost parts of the transverse lophs can similar orientations of the HSB and incipient interfaces be observed.

In *Colodon cingulatus* (Helatellidae) from the Oligocene of Montana, a similar schmelzmuster was found (Rensberger and Koenigswald, 1980), but no material for sectioning was available.

Lophiodon lautricense (Lophiodontidae), a large tapiroid from the Eocene of Europe, follows the tapiroid schmelzmuster, even though an outer zone of radial enamel occurs in some parts of the molars. The prism sheath is generally incomplete and the IPM is parallel to the prisms.

In the upper molars the horizontal HSB are widely retained. Only in the transverse lophs do the HSB turn into a vertical position. Interfaces were not seen in the available material. In the lower molars the protoconid and the hypoconid show horizontal HSB. Toward the transverse lophs, the HSB turn vertically. Interfaces are well-marked by a slight groove in the enamel surface and on the occlusal surface by an irregularity of the HSB. The lower molars have horizontal HSB which are strongly modified in the lingual walls of metaconid and entoconid.



Fig. 8.—*Tapirus priscus*, Eppelsheim, Germany, Upper Miocene. Unretouched photo of the anterior loph of the lower right M_3 with horizontal HSB in the cusps, inclined HSB in the loph and an interface in the center of the loph where the areas of protoconid (left) and metaconid (right) merge into each other. Length of bar equals 5 mm.

Heavy undulation of the HSB forms vertical structures in the outer enamel. These unusual structures resemble the modification of HSB found in hyaenids (personal observation).

Rhinocerotidae

The schmelzmuster in the molars of most rhinos (e.g., *Coelodonta antiquitatis*) consists of an inner layer of HSB and an outer layer of radial enamel. The outer layer varies considerably in different genera. It can be very thin or even missing as in *Subhyracodon* or *Floridaceras whitei*.

Rhinocerotid upper and lower molars are characterized by vertical HSB as in *Floridaceras whitei* (Fig. 7B). The vertical orientation is not restricted to certain parts of the occlusal surface as in Chalicotheriidae, Brontotheriidae, or Tapiroidea, but continues around the entire tooth and does not include any interfaces. These HSB bifurcate in the same manner as horizontal HSB. These vertical HSB have been studied by Rensberger and Koenigswald (1980) and Boyde and Fortelius (1986). The authors were not aware that this peculiar structure in rhino teeth, which results in a specific roughness of the occlusal surface, was already observed and carefully figured more than 100 years earlier by Quenstedt (1867: pl. 1:1, pl. 2:35).

In incisors the HSB are horizontal but intersect the very steep shearing facets at nearly right angles (Koenigswald, 1985; Koenigswald and Clemens, 1992). In *Coelodonta*, the prisms have incomplete prism sheaths and the IPM is mostly parallel to the prisms.

Based on the enamel surface investigation of a mandible of *Metamynodon* sp.

Table 1.—*Perissodactyl tooth material investigated in this study. 1, investigated by light microscopy on natural surfaces only; 2, investigated in sections under light microscope and SEM.*

Chalicotheriidae

Moropus elatus, Agate Springs quarries, Nebraska; Harrison Formation, Miocene; Carnegie Museum of Natural History; 1.

Moropus sp., Agate Springs quarries, Nebraska; Harrison Formation, Miocene; Carnegie Museum of Natural History; 1+2 [KOE 1436].

Chalicotherium goldfussi, Eppelsheim, Germany; Upper Miocene; Hessisches Landesmuseum, Darmstadt; 1.

Chalicotherium cf. *haberreri*, Pavlowelar, Kazakhstan; Turolian; Paleontological Museum, Moscow; 1.

Equoidea

Hyracotherium sp., Bighorn Basin, Wyoming; Willwood Formation, lower Eocene; U.S. Geological Survey, Denver; 1+2 [KOE 1022].

Equus sp., Heidenheim, Germany; upper Pleistocene; 1+2 [KOE 34].

Palaeotherium sp., Frohnstetten, Germany; Oligocene; 1+2 [KOE 1666].

Brontotheriidae

Menodus proutii, White River, Nebraska; Oligocene; Hessisches Landesmuseum, Darmstadt; 1.

large brontothere, gen. indet., Nebraska; Chadron Formation, White River Group, Nebraska; Nebraska State Museum, Lincoln; 1+2 [KOE 1637].

Tapiroidea

Tapirus priscus, Gau Weinheim, Germany; upper Miocene; Hessisches Landesmuseum, Darmstadt; 1.

Tapirus priscus, Esselborn, Germany; upper Miocene; Hessisches Landesmuseum, Darmstadt; 1.

Tapirus sp., China; Pleistocene; 1+2 [KOE 73].

Colodon cingulatus, Oligocene, Montana; Carnegie Museum of Natural History; 1.

Lophiodon lauricense, Robiac, France; late Eocene; Hessisches Landesmuseum, Darmstadt; 1.

Rhinocerotidae

Ceratotherium simum, Africa; Recent; 1+2 [KOE 610].

Rhinoceros sp., Sangiran Java; Pleistocene; 1+2 [KOE 71].

Coelodonta antiquitatis, Urspringhöhle, Germany; 1+2 [KOE 52].

Subhyracodon occidentale, M³; Museum of Comparative Zoology, Harvard University; 1+2 [KOE 356].

Floridaceras whitei, Hawthorne Formation; Miocene; Thomas Farm, Florida; Museum of Comparative Zoology, Harvard University; 1+2 [KOE 357].

(Amynodontinae), the HSB orientation and the schmelzmuster seem to follow the same pattern as Rhinocerotidae.

DISCUSSION

Hunter-Schreger bands were evolved several times in parallel among various mammalian lineages (Koenigswald and Clemens, 1992), for instance in the early Paleocene by condylarthrans (Koenigswald et al., 1987), in primates, carnivores, rodents, and a few marsupials. Despite this multiple origin, the usual orientation of HSB is horizontal. Therefore this orientation is regarded as the most primitive condition for mammals in general as well as for perissodactyls.

The interpretation of the variability of the schmelzmuster among the Perissodactyla from a phylogenetic perspective allows us to differentiate the derived genera within the various families and superfamilies, respectively. The Equoidea retain the horizontal HSB. However, when the molars become hypsodont, a significant layer of modified radial enamel is introduced between the EDJ and

the layer of HSB. This schmelzmuster developed convergently in several other large herbivores with hypsodont molars (Pfretzschner, in press; Koenigswald et al., 1993). These large herbivores share the characteristic of having the IPM at a high (close to 90°) angle with the prisms.

Other Perissodactyla, such as Brontotheriidae, Chalicotheriidae, Tapiroidea, and Rhinocerotidae, follow different pathways of modification in their schmelzmuster. Brontotheriidae, widely accepted to be closely related to Equoidea, keep the crystallites of the IPM parallel to the prisms and develop the U-shaped orientation of the HSB. The strongly curved HSB intersect the occlusal surface at almost right angles. They share this derived character with the Chalicotheriidae. Differences between some Chalicotheriidae and Brontotheriidae are expressed mainly in the thickness of the outer radial enamel. Whether the very similar orientation of the HSB in both families is a synapomorphy must be tested by a larger survey of the schmelzmuster in both groups.

In Tapiroidea the HSB turn in a vertical direction only in the transverse lophs immediately below the crest. *Tapirus* and *Lophiodon* differ in the enamel on the lingual side of the lower molars.

The Rhinocerotidae have a very derived schmelzmuster with vertical HSB. The vertical orientation of HSB in Rhinocerotidae is unique among Perissodactyla. However, a similar orientation evolved convergently in astrapotheres (Fortelius, 1984, 1985; Rensberger and Pfretzschner, 1992), but not in *Arsinoitherium* as assumed by Fortelius (1984) and since disproven by Pfretzschner (in press).

Whereas in the Rhinocerotidae the HSB are vertical around the entire molars, in tapirs, chalicotheres, and brontotheres, the HSB of the various cusps developed vertical HSB individually. The interfaces, found as distinct lines between the cusps even when they are united in the same loph, are the most obvious feature indicating this different strategy.

Hyracoidea, which are regarded by some as a sister group of the Perissodactyla (Fischer, 1986), have a horizontal HSB orientation in some genera (Fortelius, 1985), but, astonishingly, most genera lack HSB altogether.

A strong functional significance of the modified orientation of the HSB in perissodactyls is indicated first by the restriction of the modifications to the main cutting edges, and second by the parallel occurrence of this tendency in several lineages such as in Chalicotheriidae, Brontotheriidae, Tapiroidea, and Rhinocerotidae. The functional significance here is that the HSB intersect the main shearing facets at almost right angles. The modified orientation of HSB brings a large number of prisms into a direction favorable for reduced wear (Rensberger and Koenigswald, 1980; Boyde and Fortelius, 1986). This modification has reached its greatest perfection in the Rhinocerotidae, but is not found in Equoidea or any member of the Artiodactyla.

Even if the teeth are to some extent worn, the high angle between the cutting edge and the HSB is maintained in chalicotheres and brontotheres and especially in Rhinos.

Three apparently antagonistic hypotheses were formulated to explain the adaptive significance of vertical HSB in Rhinocerotidae. Rensberger and Koenigswald (1980) argued that the vertical HSB allow a maximum number of prisms to intersect the occlusal surface at almost right angles. Their experimental data demonstrated that there is less abrasion of the enamel when prisms are at right angles to the occlusal surface compared to prisms parallel to the occlusal surface. Pfretzschner (1992, in press) argues that vertical HSB would ideally compensate mas-

tatory stresses in the enamel of hypsodont teeth near the EDJ. Rensberger (1992), on the other hand, argues that the maximum tensile stresses in the flat lophs of rhinos are normal to the cutting edges, causing fracturing parallel to the edges. Orientation of the HSB perpendicular to these edges resists such fracturing. The material studied here makes it possible for us to evaluate these hypotheses.

Vertical HSB were achieved in Rhinocerotidae and Astrapotheriidae in low-crowned molars. Since this character antedates hypsodonty in both lineages, it cannot be an adaptation specifically related to hypsodonty. Vertical HSB, which are found to reduce abrasion in the cutting edges, are not unique to Perissodactyla. A similar orientation of HSB as in Tapiroidea has been found in the carnassials of some Carnivora, in which the horizontal HSB change direction abruptly when they approach the cutting edge to intersect the blades of the carnassial notch vertically.

There is a general demand to stabilize the cutting edges, especially in low-crowned teeth, to keep the functional apparatus in shape. Wear of the oblique cutting edges in low-crowned teeth, in Chalicotheriidae and in Brontotheriidae but also in Carnivora, changes the morphology of teeth significantly and demands a readjustment of the antagonist. The specific quality of high-crowned teeth is that, due to the almost vertical cutting edges, the morphology of the occlusal surface is maintained during progressive wear for a relatively long time. If wear of cutting edges is reduced by prisms penetrating at high angles (as in vertical HSB), a strong selective pressure applies to HSB reorientation from horizontal to U-shaped or vertical.

However, this explanation does not contradict the hypothesis of Pfretzschner (in press). The animals with vertical HSB in the entire molars, such as the early, low-crowned Rhinocerotidae, have an appropriate prerequisite to build hypsodont molars. This prerequisite is present in the Rhinocerotidae and the Astrapotheriidae. According to Pfretzschner's hypothesis, most other herbivores, like horses or bovids, that evolved hypsodont molars but retained horizontal HSB introduced the "modified radial enamel" close to the EDJ. In the modified radial enamel, thick layers of IPM lie between rows of prisms. These layers therefore were called "inter row sheets" by Boyde (1964). It is mechanically important that the crystallites of the IPM are at a high angle to the prisms. The thick descending layers of IPM in the modified radial enamel and the rows of ascending prisms function very similarly to vertical HSB. The orientation of structural elements is very important since the enamel is very anisotropic in its physical properties.

Among small mammals, some rodent lineages modify the enamel of their incisors from primarily horizontal uniserial HSB to vertical HSB. Several different pathways to achieve this character can be distinguished in the Myoxidae, Dipodidae, and Spalacidae (Koenigswald, 1993). The functional significance of these modifications in the very thin rodent enamel is not yet fully understood. The uniserial HSB with an IPM at right angles to the bands seems to be functionally more isotropic to crack propagation than the thick HSB of the larger mammals.

Modification of the primarily horizontal HSB occurs only occasionally among large mammals. The occurrence in Perissodactyla is unusually frequent. Obviously, with exception of Equoidea, most other groups in the Perissodactyla change HSB orientation instead of introducing a large angle between the IPM and the prisms. They share this character with astrapotheres. Therefore, the modification of HSB orientation seems to be linked to IPM parallel to the prisms. In contrast to the modified radial enamel, which is linked to the ability to reorient the crys-

tallites of the IPM at an angle to the prisms, the lateral reorientation of the HSB demonstrates second pathway to strengthen the enamel in cases when IPM crystallite orientation cannot be changed.

This study of HSB orientation in *Perissodactyla* demonstrates that the quality of enamel is a source of functional as well as phylogenetic information. Neither aspect excludes the other since the evolution of characteristics always has to have some functional significance if the new combination of characteristics is to be advantageous for the animal. It is especially true in enamel that many characteristics evolved in parallel in various lineages that indicate such functional aspects. On the other hand, different groups often solve similar functional problems in different pathways. This allows us to identify taxonomic groups of higher rank, e.g., at the genus or family level.

ACKNOWLEDGMENTS

I am very indebted to M. R. Dawson, Carnegie Museum of Natural History, for providing the material of *Moropus* and for her hospitality during my stay in Pittsburgh. Further material was kindly provided by R. M. Hunt, Jr., Nebraska State Museum, Lincoln, and F. Schrenk, Darmstadt. For intensive discussions, I thank M. Sander and H. U. Pfretzschner, Bonn. The latter gave permission to refer to his unpublished paper. Furthermore, two anonymous reviewers contributed to the clarity of the discussion. I thank W. Haas who kindly helped photograph the HSB in some critical specimens. D. Kranz and G. Oleschinski provided the photos and the artwork. Finally, I am very grateful to M. Sander, C. Gee, and Th. Hansen for bringing the English into readable form.

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FIVE NEW SPECIES OF *HYDROPTILA* FROM EASTERN UNITED STATES (INSECTA: TRICHOPTERA: HYDROPTILIDAE)

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ABSTRACT

Five new species of *Hydroptila* from the eastern United States similar to *H. strepha* Ross are described and figured: *Hydroptila antennopedia* and *H. parachelops* from Pennsylvania, New Hampshire, and Maine; *H. morsei* from South Carolina, Texas, and Florida; *H. blicklei* from Maine; *H. holzenthali* from Mississippi. Male genitalia of *H. strepha*, determined to occur only in Pennsylvania and West Virginia, are illustrated.

INTRODUCTION

The United States Army Corps of Engineers (Pittsburgh District) has supported our ongoing study of caddisflies in reservoir tailwaters of the upper Ohio River drainage basin. As part of this project, ultraviolet light traps were operated monthly from May through October at the outflow from Youghiogheny River Lake in southwestern Pennsylvania (J. L. Sykora, unpubl. reports to U.S. Army Corps of Engineers). Of the more than 100 species collected, two were tentatively identified as *Hydroptila strepha* Ross. Comparisons of the genitalia of the specimens collected from the Youghiogheny River to the figures of *H. strepha* suggested differences, prompting an examination of the holotype of *H. strepha* collected from the Susquehanna River in Pennsylvania. Close examination indicated that the specimens from the Youghiogheny River represented two new species closely related to *H. strepha* and other members of the *H. consimilis* group of Marshall (1979).

The discovery of two new species similar to *H. strepha* suggested that reexamination of the species was in order. The question of the identity of *H. strepha* was reinforced by the unusual distribution pattern for the species, with records from the northeastern United States, Minnesota, Mississippi, Texas, and South Carolina. Therefore, an effort was made to secure additional *H. strepha* material. Collections of specimens identified as *H. strepha* and related species were obtained from the University of New Hampshire, Clemson University, Illinois Natural History Survey, National Museum of Natural History, University of North Texas, University of Tennessee, and University of Minnesota. Specimens from these collections were compared with the holotype of *H. strepha* resulting in the identification of three additional new species: one from Mississippi; one from Maine; and another from South Carolina, Texas, and Florida. The material available to us indicates *H. strepha* is known only from Pennsylvania and West Virginia.

The genus *Hydroptila* is the largest and most successful of the family Hydrop-

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Submitted 9 April 1993.

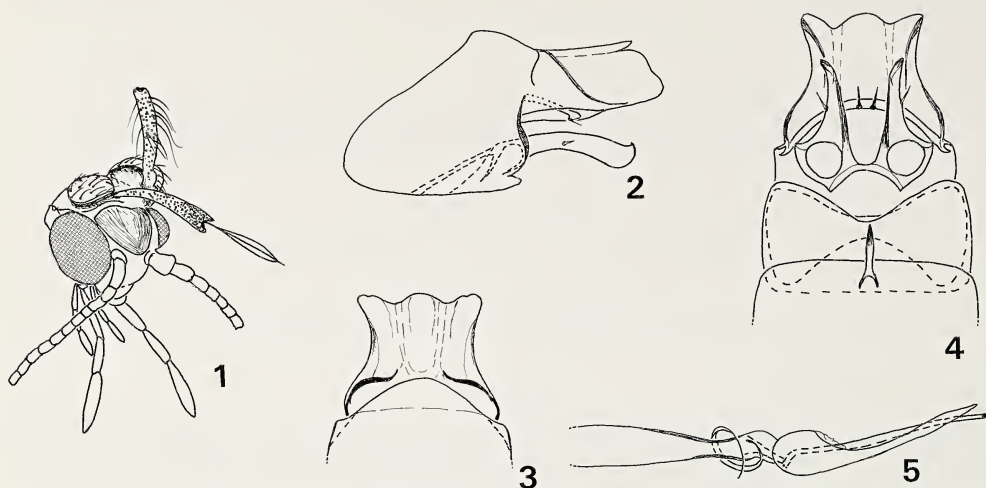


Fig. 1-5.—*Hydroptila antennopedia*, new species: 1, head of paratype; 2, male genitalia, lateral view; 3, tenth abdominal segment, dorsal view; 4, male genitalia, ventral view; 5, phallus, dorsal view.

tilidae with world-wide, cosmopolitan distribution (excluding polar regions). Marshall (1979) estimated that this genus included over 150 species worldwide. Since that time, many more species have been described from different parts of the world. Up to 1979, 60 species were recorded by Blickle (1979) in the continental United States, a number that has been constantly growing. Of these new species many were discovered in the southern United States. At present, 95 *Hydroptila* species are known from the continental United States, 72 of which are described from the eastern United States and, according to Masteller and Flint (1992), 27 species of *Hydroptila* are known from Pennsylvania.

Marshall (1979) recognized several species-groups which are characterized by male genitalia. Species described in this paper are members of the widely distributed *consimilis* group. Terminology utilized in the descriptions follows that of Marshall (1979).

Specimens are deposited at the Carnegie Museum of Natural History (CMNH), the Department of Entomology, Clemson University (CU), the Department of Entomology, University of New Hampshire (NH), the Illinois Natural History Survey (INHS), the University of Minnesota (UM), the National Museum of Natural History (NMNH), or in the junior author's collection (SCH).

Hydroptila antennopedia, new species
(Fig. 1-5)

Diagnosis.—This species is distinguished from any other known species of *Hydroptila* by a combination of features in the male genitalia. Segment X is trilobed; the inferior appendages expand gradually toward a rounded apex with a dorsoapical point; and the apical section of the phallus is divided posteriorly into two sections of equal length.

Description.—Male: Length 2.1 mm. Antennae 34-segmented. Color brown in alcohol. Sternite of abdominal segment VII with short, pointed process; segment VIII annular, quadrate from lateral view; segment IX with blunt, broad dorsal lobe, and a narrow mediolateral projection. Dorsal aspect of segment X broad, three-lobed with central lobe rounded at apex, lateral aspect almost rectangular with oblique apical margin. Subgenital plate shorter than inferior appendages, rounded at apex and

bearing two short spines close to the apical margin. Inferior appendages in lateral view with slightly sinuate ventral and dorsal margins, expanding into a ventrally rounded apex with a distinct dorsoapical point; ventral aspect with a quadrangular broad base and narrow, triangular apical section. Phallus relatively short, distal section divided into two narrow, long processes, the dorsal one produced from a broad cup-shaped base, the ventral process a rod-shaped continuation of the ejaculatory duct; short paramere arising anteriorly of neck making full revolution.

Female.—Unknown.

Type Specimens.—Holotype, male (CMNH): PENNSYLVANIA, Fayette Co., Youghiogheny River Lake outflow near Confluence, June 17–18, 1991, light trap. Paratypes: The specimens made available to us and identified as *H. antennopodia* included many examples from Pennsylvania, New Hampshire, Maine, and one specimen from Minnesota. PENNSYLVANIA, Fayette Co., Youghiogheny River Lake outflow near Confluence 1 male (SCH); same August 24–25, 1991, 1 male (CMNH); Forest Co., Otter Run, July 1, 1990, E. C. Masteller, 5 males; Warren Co., 2 mi S Warren, 25 June 1987, O. S. Flint, Jr., 2 males (NMNH). MAINE, Allagash, July 5, 1959, 5 males; same July 6, 1959, 4 males; same July 8, 1959, 2 males; same July 10, 1959, 40 males; same July 13, 1959, 8 males; same July 19, 1959, 39 males; same July 22, 1959, 17 males; same July 23, 1959, 9 males; same July 24, 1959, 4 males; same July 25, 1959, 21 males; same July 26, 1959, 69 males; same July 27, 1959, 22 males; same July 29, 1959, 90 males; same July 30, 189 males; same August 1, 1959, 186 males; same August 2, 1959, 1 male. Dennistown, July 22, 1959, 1 male; same August 27, 1959, 1 male; Kingfield, August 13, 1964, 40 males; Round Pond, July 13, 1959, 1 male (NH); Allagash, July 13, 1959, 1 male; same July 29, 1959, 1 male; same August 1, 1959, 10 males; same August 2, 1959, 11 males; Big Black River, July 25, 1961, A. Brower, 120 males; Oxbow, July 22, 1961, A. Brower, 1 male (NMNH). MINNESOTA, Finland Co., July 25, 1965, D. Etnier, 1 male (UM). NEW HAMPSHIRE, Colebrook, July 17–24, 1957, 2 males; same July 10–17, 1957, 1 male (NH).

Remarks.—One paratype of *H. antennopodia* bears a pair of thin, leg-like appendages extending from beneath the “scent caps” (Fig. 1). According to Schmid (1980) who illustrated similar appendages in *H. ampoda*, these erectile organs may carry androconia in the setae or scales with odoriferous function. This new species is placed near *H. strepha* Ross (1941) based on the trilobed segment X and the short, pointed apical sections of the phallus. It differs in the shape of inferior appendages which are tubular in *H. strepha*, but club-shaped in *H. antennopodia*. All the specimens designated as paratypes from Maine were previously identified as *H. strepha* (Blickle, 1964). Morse and Blickle (1957) also reported *H. strepha* from New Hampshire. Based on our reexamination, it is quite possible that *H. strepha* does not occur in New Hampshire and Maine. The material available to us indicates that *H. strepha* is known from the original locality in north-central Pennsylvania (Susquehanna River) and West Virginia (Pendleton County, Smoke Hole State Park, Briggs Run, April 9, 1977, Don and Mignon Davis, Det. Flint; Pendleton County, Smoke Hole Camp, May 14, 1963, Field and Flint, 1 male). As considerable confusion exists in the identity of *H. strepha*, the species is redrawn from the type (Fig. 6–9).

Etymology.—Latin, meaning leg-like antennae.

Hydroptila parachelops, new species
(Fig. 10–13)

Diagnosis.—This species is distinguished by a combination of several morphological characters of male genitalia. These include the trilobed segment X with

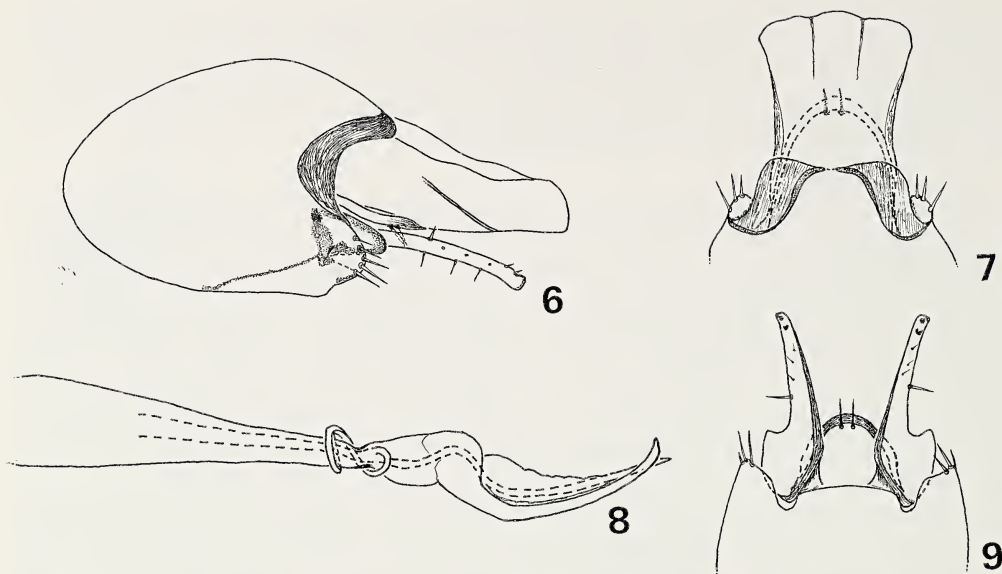


Fig. 6-9.—Male genitalia of *Hydroptila strepha* Ross: 6, lateral view; 7, tenth abdominal segment, dorsal view; 8, phallus, dorsal view; 9, inferior appendages, ventral view.

very small central lobe and large lateral lobes, ventrally curved, tubular inferior appendages and long, biramose apical section of the phallus.

Description.—Male: Length 3.0 mm. Antenna 29-segmented. Brown in alcohol. Sternite of segment VII with short, pointed apicomeres process; segment VIII tubular with straight apical margins and covered with sparse setae; segment IX emarginate ventrally and dorsally with relatively short ventro-lateral extensions; segment X with dorsal aspect wide at the base and slightly narrowed at the excised, flared apex; central lobe small and membranous, lateral sections slightly sclerotized, wide in the middle, tapering posteriorly. Inferior appendages from lateral view almost tube-shaped, long and narrow, curved ventrally, with slightly enlarged distal section, and rounded apex; ventral view triangular with broad base and straight mesal margins, the distal section rapidly tapering towards obtuse apex with small, sclerotized lateral point. Subgenital plate round with sclerotized ventral “strip” bearing two setae and a membranous dorsal section. Phallus with relatively short base, forked distal section; dorsal portion heavily sclerotized and curved with apex pointed ventrally; ventral branch narrow, parallel-sided, lightly sclerotized and bent at the base; neck with paramere making at least one full revolution, ejaculatory duct sinuous in neck, continuing into ventral branch of the phallus.

Female.—Unknown.

Type Specimens.—Holotype, male (CMNH): PENNSYLVANIA, Fayette Co., Youghiogheny River Lake outflow near Confluence, Pennsylvania, August 24–25, 1991, light trap. Paratypes: same, 1 male (SCH); MAINE, Dennistown, July 31, 1959, 5 males (INHS); same, July 19, 1959, 2 males; same July 25, 1959, 13 males; Oquossoc, July 28, 1959, 1 male; same July 30, 1959, 2 males; same July 31, 1959, 1 male (NH).

Remarks.—*Hydroptila parachelops* is closely related to *H. strepha* Ross (1941) and *H. chelops* Harris (1985), on the basis of trilobed segment X, tube-shaped inferior appendages, and forked distal section of phallus with curved apex. It differs from the latter in the shape of forked phallus which has only one sclerotized apical branch. From the former it could be distinguished by the triangular, ventral aspect of inferior appendages with straight mesal margins similar to *H. arctica*

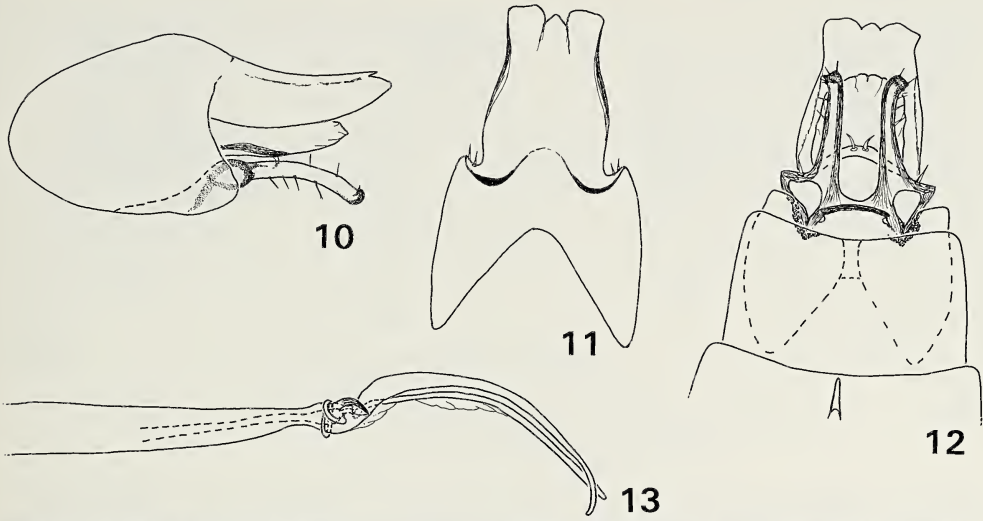


Fig. 10-13.—Male genitalia of *Hydroptila parachelops*, new species: 10, lateral view; 11, tenth abdominal segment, dorsal view; 12, ventral view; 13, phallus, dorsal view.

Ross (1938). Those specimens of *H. parachelops* collected in Maine and obtained from the Illinois Natural History Survey and the University of New Hampshire collections were previously identified as *H. strepha*.

Etymology.—Latin, close to *chelops*.

Hydroptila morsei, new species
(Fig. 14-17)

Diagnosis.—This species is characterized by male genitalia with segment IX extended anteriorly into a ligament attached to segment VIII, trilobed segment X bearing sickle-shaped lateral lobes, rod-shaped inferior appendages and membranous apex of phallus with sinuous tip.

Description.—Male: Length 2.1 mm. Antennae 28-segmented. Color light brown in alcohol. Venter of abdominal segment VII with short apicomeral projection; segment VIII tubular with rounded posteroventral edges. Segment IX recessed within segment VIII, in lateral aspect rounded anteriorly with anteroventral margin extended into sclerotized ligament-like section attached to the posteroventral margin of segment VIII. Dorsal aspect of segment X trilobed with broad central lobe and sclerotized lateral lobes flared and sickle-shaped; in lateral view broadly truncate with apex of the lateral lobes upturned. Subgenital plate membranous and extending over the midlength of inferior appendages, rounded apically and bearing two short setae. Inferior appendages in lateral aspect almost as long as segment X, rod shaped, in ventral view each with broad triangular base with short lateral spines. Phallus with proximal section broad and slightly longer than the distal portion; distal section membranous with a slightly curved tip and bulbous base encircled by a short spiral paramere making one full revolution.

Female.—Unknown.

Type Specimens.—Holotype, male (CU): SOUTH CAROLINA, Dorchester Co., Four Holes Swamp, Goodsons Lake, 13 August 1976, J. Morse. Paratypes: same, 4 males (3 males in CU, 1 male in SCH); Berkeley Co., Four Holes Swamp, Mims Lake, 7 May 1976, J. Morse, 2 males (1 male in CU, 1 male in CMNH); TEXAS, Hardin Co., Cypress Creek, off TX 326, N. Kountze, UV light, October 23, 1992, Moulton and Alexander, 6 males; Hardin Co., Hickory Creek, off US

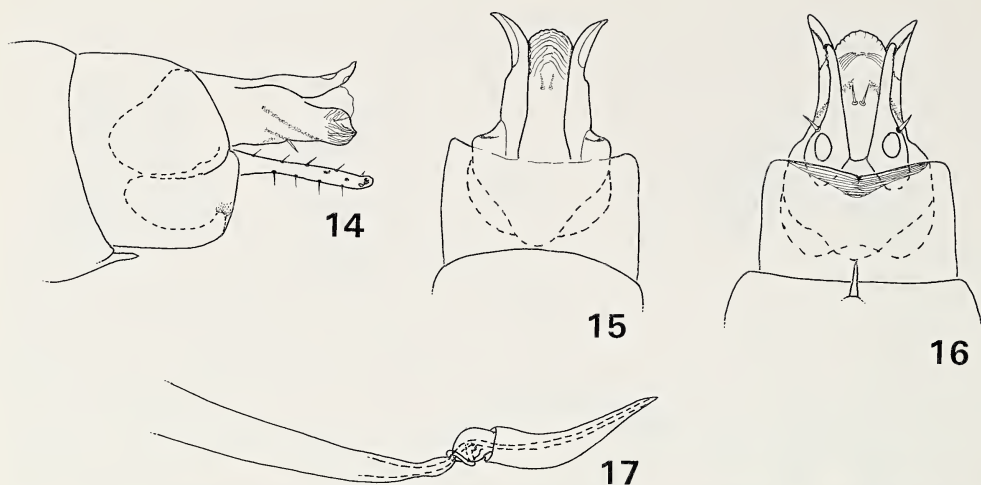


Fig. 14–17.—Male genitalia of *Hydroptila morsei*, new species: 14, lateral view; 15, dorsal view; 16, ventral view; 17, phallus, dorsal view.

287/69, N. Kountze, October 23, 1992, UV light, Moulton and Alexander, 1 male (SCH); FLORIDA, Highlands Co., Archbold Biological Station, March 6, 1964, S. W. Frost, 2 males (NMNH).

Remarks.—*Hydroptila morsei* is closely related to *H. strepha* Ross (1941) but it is distinguished by the shape of segment X and the phallus. In *H. morsei*, the distal portion of the tenth segment is characterized by well-developed lateral lobes separated from a large central section by deep incisions while in *H. strepha* these incisions are shallow and the central section is small. In *H. strepha* the distal portion of the phallus has a broad, sclerotized base extending into the lateral, chitinized margin with a membranous lateral part. In *H. morsei* the section surrounding the ejaculatory duct is entirely membranous. This species was collected from five sites located in South Carolina, Texas, and Florida. It was not recorded by Harris et al. (1991) from Alabama and its distribution in the southern United States remains unclear.

Etymology.—Named in honor of Dr. John Morse who collected this species.

Hydroptila blicklei, new species
(Fig. 18–21)

Diagnosis.—The male of this species is characterized by the combination of several characters. The inferior appendages are wide at the base extending distally to pointed, divergent apices; segment X is trilobed with rounded central lobe slightly protruding dorsad and a pair of pointed, divergent lateral lobes; ventral aspect of subgenital plate with “X”-shaped sclerotized central section; phallus membranous with a short spiral paramere.

Description.—Male: Length 2.1 mm. Antennae broken off. Color yellowish-brown in alcohol. Sternite of abdominal segment VII with short, pointed apicomeral process; segment VIII generally quadrate with slightly excised posteroventral margin and rounded ventrolateral aspect; segment IX retracted into VIII, triangular from lateral view with spoon-shaped ventral extensions and incised posteroventral margin; apex of segment X divided into three lobes, a membranous apically rounded mesal lobe and a pair of sharp sickle-shaped lateral lobes; subgenital plate from lateral view partially sclerotized,

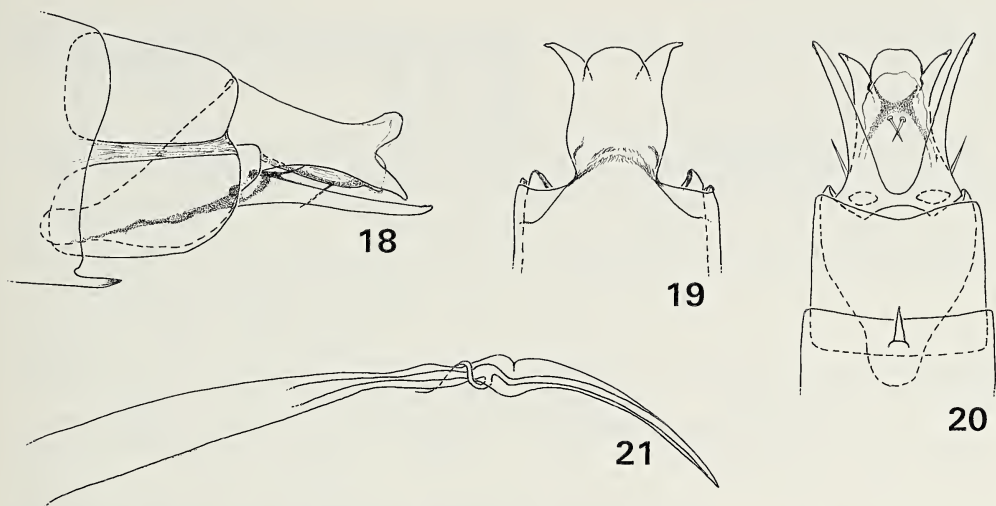


Fig. 18–21.—Male genitalia of *Hydroptila blicklei*, new species: 18, lateral view; 19, tenth abdominal segment, dorsal view; 20, ventral view; 21, phallus, dorsal view.

almost as long as segment X and extending over midlength of inferior appendages, ventrally with “X”-shaped, sclerotized section, bearing a pair of setae centrally; inferior appendages longer than segment X, in lateral view elongated, narrowly triangular and gradually tapering toward pointed tips, in ventral aspect with a broad base extending into blade-shaped apices diverging distally; phallus curved ventrally, central portion narrow tapering to a long neck, distal section membranous almost triangular from dorsal view with slightly curved apex, ejaculatory duct sinuous in the neck and continuing through the apical, membranous section with a slender, spiral paramere arising anteriorly of neck making slightly more than one full revolution.

Female.—Unknown.

Type Specimens.—Holotype, male (NH): MAINE, Dennistown, July 29, 1959. Paratypes: MAINE, Oquossoc, July 31, 1959, 1 male (NH); Oxbow, July 22, 1961, A. Brower, 10 males (NMNH).

Remarks.—This species is another member of the *H. consimilis* group closely related to *H. strepha* Ross (1941) and *H. roberta* Hamilton and Holzenthal (1986). It differs from the former by the lateral aspect of inferior appendages which are straight in *H. blicklei* and curved in *H. strepha*. From the latter it could be distinguished by the phallus with spiral paramere, trilobed tenth segment with membranous mesal section and by segment IX with spoon-shaped anteroventral section. These specimens collected by Dr. A. E. Brower were made available to us by Dr. J. S. Weaver, Jr. III and Dr. O. S. Flint, Jr. They were originally identified as *H. strepha* (Blickle, 1964).

Etymology.—Named for Dr. R. L. Blickle who first studied this species.

Hydroptila holzenthali, new species
(Fig. 22–25)

Diagnosis.—The male of this species is characterized by the combination of several characters, including bilobed segment X, triangular subgenital plate with two apical lobes bearing terminal setae, wedge-shaped inferior appendages, and the very long, thin and tubular phallus.

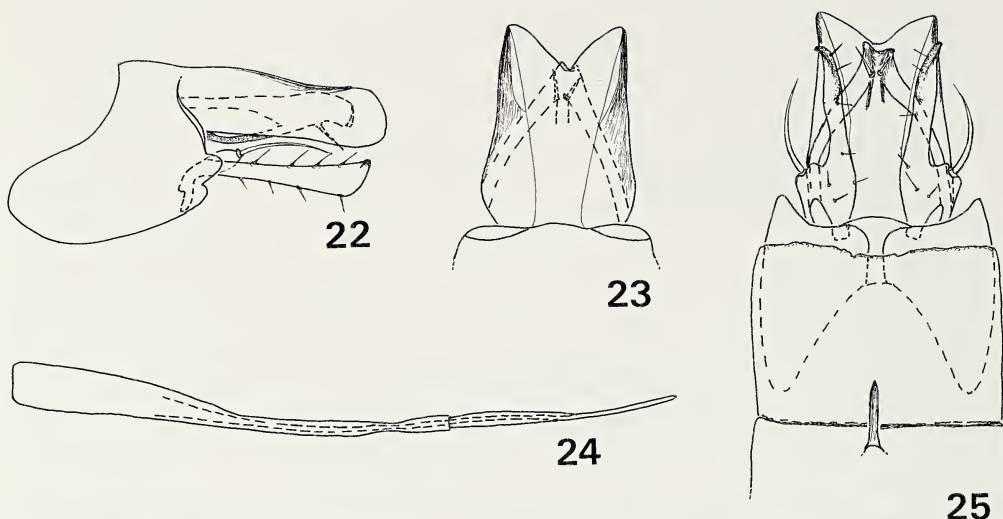


Fig. 22–25.—Male genitalia of *Hydroptila holzenthali*, new species: 22, lateral view; 23, tenth abdominal segment, dorsal view; 24, phallus, dorsal view (40% reduction); 25, ventral view.

Description.—Male: Length 3 mm, antennae broken off, color light brown in alcohol. Posteroventral margin of segment VII with short apicomeres process. Segment VIII tubular, posteroventral margin irregular with rounded posteroventral corners. Segment IX heavily sclerotized, in lateral view with rounded anteroventral section extending deeply into segment VIII; dorsal and ventral aspects widely incised. Segment X in dorsal view bilobed, lobes flared, in lateral view rectangular and broad with rounded apex. Subgenital plate membranous, triangular, incised in the middle, almost as long as inferior appendages, apex divided into two short lobes bearing two setae. Inferior appendages almost as long as segment X, in lateral view wedge-shaped, with posteroventral corners rounded, dorsal margin ending in small posterodorsal point; in ventral view widely separated at broad, shouldered quadrangular bases with a long and prominent seta located at rounded posterolateral corner. Tubular phallus very long, extending over more than three segments, with funnel-shaped base constricted at midlength without spiral paramere and with one third of ejaculatory duct protruding freely from membranous sheath.

Female.—Unknown.

Type Specimen.—Holotype, male (CU): MISSISSIPPI, Stone Co., Flint Creek, Hwy 26, 7.9 km E Wiggins, 7 June 1979, Col. R. W. Holzenthall.

Remarks.—The holotype of this species was collected in Mississippi and originally identified as *H. strepha* (Harris et al., 1982). *Hydroptila holzenthali* is closely related to *H. quinola* Ross (1947). It is distinguished by the absence of defined thumb-like projections on the base of inferior appendages, and a membranous and quadrangular subgenital plate. In addition, the apices of inferior appendages in *H. holzenthali* are slightly hooked while in *H. quinola* the apices are rounded.

Etymology.—Named for Dr. Ralph W. Holzenthall, University of Minnesota who collected the holotype.

ACKNOWLEDGMENTS

This project was supported by contract DACW 5991M0705 from the U.S. Army Corps of Engineers, Pittsburgh District, Pittsburgh, Pennsylvania. Special thanks go to J. M. Fowles and M. Koryak from the U.S. Army Corps of Engineers for their assistance in the selection of sites, logistics of sample collection, and critical review of the manuscript. We also acknowledge the help of O. S. Flint, Jr., National Museum of Natural History, J. Morse, Clemson University, and J. S. Weaver, Jr. III, who

provided us with additional specimens of *Hydroptila*. The type of *H. strepha* was loaned for use in this study by the Illinois Natural History Survey.

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DESCRIPTION OF THE IMMATURE STAGES OF SIX SPECIES OF
SPHAENOGNATHUS, WITH COMPARATIVE NOTES ON
PHYLOGENY AND NATURAL HISTORY
(INSECTA: COLEOPTERA: LUCANIDAE)

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ABSTRACT

Third instar larvae of six Andean species of *Sphaenognathus* and pupae of *Sphaenognathus lindenii* are described and illustrated, with comparative notes on larvae of the related genus *Chiasognathus*. Keys are provided to larvae of genera of Chiasognathini and to species of *Sphaenognathus* for which larvae are known. A character considered diagnostic for Chiasognathini is to have all setae on the raster uniformly inclined laterally. The absence of a basal tooth on the mandible in *Sphaenognathus peruvianus* supports its placement in the subgenus *Chiasognathinus*. Derived larval characters are presented to support three monophyletic taxa: the tribe Chiasognathini, the genus *Sphaenognathus*, and a species-group containing *S. lindenii*, *S. oberon*, and *S. metallifer*.

INTRODUCTION

The family Lucanidae is of worldwide distribution and includes about a thousand described species (Benesh, 1960). According to Blackwelder (1944), there are 128 species in the Neotropical region. The larvae of several species of Lucanidae have been described. Significant publications on larvae of this group include Hayes (1929), Van Emden (1935, 1941, 1952), Medvedev (1952), Ritcher (1966) and Alderson (1975*a*, 1975*b*). In the Neotropical region, larvae of only four species have been described: *Sclerostomus ruficollis* Luederwaldt, *Pholidotus spixi* Nagel, *Pycnosiphorus femoralis* (Guérin), and *Chiasognathus granti* Stephens (Nagel, 1934; Cekalovic, 1982; Cekalovic and Castro, 1983; Costa et al., 1988). Most lucanid larvae live in decaying logs (Arnett, 1973; Borror et al., 1981), but the larvae of at least one species live in the soil (Milne, 1933).

The larvae described in the present work are in the tribe Chiasognathini, represented by *Chiasognathus* and *Sphaenognathus*. At present, according to Benesh (1990) and incorporating the synonymies made by Lacroix (1969), *Chiasognathus* includes four species, all from Chile. *Sphaenognathus* includes about 40 Neotropical species (Bartolozzi et al., 1992) and an additional species from Australia described by Moore (1978), thus implying a Gondwanian distribution for the tribe with ancient connections across Antarctica.

The only species of the tribe for which the larva has been described is *Chiasognathus granti* Stephens (Cekalovic and Castro, 1983). Notes on adults of *Chiasognathus* were published by Montalegre (1925), Ureta (1934), and Mathis (1981); information on the adults of *Sphaenognathus* was provided by Howden and Campbell (1974), Perrault (1991), Bartolozzi et al. (1992), and Bartolozzi and Onore (1993). The phylogeny of Lucanidae based on adults was discussed by

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Submitted 20 May 1993.

Holloway (1960, 1968, 1969), Lacroix (1969), and Howden and Lawrence (1974). Phylogenetic hypotheses based on larvae were discussed by Van Emden (1952) and Lawrence (1981).

MATERIALS AND METHODS

To collect larvae, soil was sampled in areas where adults had been found. The soil was dug to a depth of 20 cm, and larvae, pupae, and associated adults were collected. Intact larvae were fixed by boiling gently in water for 3–5 min, and then preserved in 80% ethanol. The pupae were maintained alive in moist boxes until they became adults that were then killed and mounted for identification.

To study the larvae, the mandibles were removed using two strong needles, and then successively the labium and maxillae were removed using scissors. Larval structures submerged in 80% ethanol were examined at 50× with a stereomicroscope. The determination of sex in larvae was made by the presence (male) or absence (female) of Herold's organs as described by Menees (1957). The shape of the last two antennomeres and number and position of teeth of the stridulatory organs of the mesothoracic and metathoracic legs were used as characters to identify the larvae to genus. To distinguish species the following characters were used: number of teeth on the left mandible, shape of epipharyngeal pterotormae, shape of the prothoracic lateral sclerome, number of teeth on plectrum and pars stridens, shape of the thoracic spiracle and setation of lateral anal lobes and raster. The terminology used follows that of Edwards (1930), Böving (1936), Ritcher (1966) and Britton (1970).

I borrowed material from the following institutions or persons: CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CV, Carlota Vergara Collection, Santiago, Chile; FSCA, Florida State Collection of Arthropods, Gainesville, Florida, USA; IZAV, Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela; OSUO, Department of Entomology Collection, Oregon State University, Corvallis, Oregon, USA; QCAZ, Museo del Departamento de Biología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador; WSUC, James Entomological Collection, Washington State University, Pullman, Washington, USA.

NATURAL HISTORY

In 1986, L. Coloma found a great number of adults of *Sphaenognathus oberon* in Casha Totoras, Bolivar Province, Ecuador. With the intention of finding larvae of this stag beetle in the vicinity, I searched carefully in rotten logs and old stumps. No larvae were found in rotting wood, so I extended the search to the soil where digging and sifting soon revealed several larvae of *S. oberon*. Investigating the same habitat at other localities, I found the larvae of *S. lindenii*, *S. metallifer*, *S. nobilis*, *S. peruvianus* (Fig. 1), and *S. subtilis*.

I never found eggs in the natural habitat, so in March, 1988, I dissected a dozen freshly killed females. These contained immature eggs in various stages of development. The number of eggs varied from 12–96. First instar larvae were found in groups up to a maximum of 54 individuals. They were in the first 3–10 cm of topsoil which was rich in humus and roots. Very often a dead female was found buried in the soil close to the group of larvae. Species of plants typically found growing in the topsoil near larvae were: *Salpichroa* sp. (Solanaceae), *Gynoxys buxifolia* (Asteraceae), *Orthrosanthus chimboracensis* (Iridaceae), *Equisetum bogotense* (Equisetaceae), *Barnadesia spinosa* (Asteraceae), *Hypericum laricifolium* (Hypericaceae), *Lachemilla orbiculata* (Rosaceae), *Ribes andicola* (Saxifragaceae), *Hesperomeles pernettifolia* (Rosaceae), *Chusquea* sp. (Poaceae), and *Elaphoglossum* sp. (Lomariopsidaceae).

Second instar larvae were less frequently encountered in the soil than third instar larvae. Third instar larvae were distributed uniformly, roughly equidistant from one another. They were buried 10–20 cm deep, and there was a maximum of 36 specimens per square meter. In some areas larvae were numerous, while in other, apparently identical, sites no larvae were found. In uniform habitat, the females may be arbitrary when choosing oviposition sites. Perhaps they settle

when they encounter some obstruction to flight, such as small bushes, and then lay their eggs.

Soil and fragments of roots were found in dissections of the gut, thus indicating that larvae may eat decomposing organic materials mixed with soil and small roots. When dug from the soil, larvae rolled into the characteristic C-shape of scarabaeiform larvae and remained inactive. Specimens unearthed at dusk and left on the surface were found in the same place the following morning. As the sun came up, they desiccated and died. Unearthed larvae of *S. lindenii* have the terga of abdominal segments 3–5 covered with moist soil, suggesting some special property of the cuticle or some secretion in those specific areas. I observed the same phenomenon in recently uncovered larvae of *Sphaenognathus oberon* and *S. metallifer*.

When disturbed, the larvae of *S. lindenii* produced vibrations using a stridulatory apparatus. Simultaneously and rhythmically, the metathoracic trochanter was rubbed against the mesothoracic coxa. No sound audible to human ears was produced, but vibrations could be felt when the stridulating larvae was held in hand. The stridulation may be used by larvae for protecting or marking the territory where they feed, as suggested by the evenly spaced distribution of larvae in the soil. Mature third instar larvae were 10–20 cm deep in suboval cavities with internal dimensions about 35 by 70 mm. Sometimes these cavities contained numerous white Collembola. I found dead larvae in the soil, covered by a white fungus. Others were full of brown liquid and very soft. One contained a dipteran puparium. Close to farms, domestic pigs actively dig the soil searching for the white grubs, which they eat voraciously. Dogs also follow farmers when they are preparing or plowing the soil, eating the larvae, pupae, and adults as they are turned up.

Pupae were in cavities as described above, each with its larval exuvium retracted to the caudal end. The pupae (Fig. 50–52) reposed on their dorsal surfaces and rotated their abdomens when disturbed. Pupae were found in the soil from November to February and adults from December to March. First, second, and third instar larvae, however, were found throughout the year, suggesting a life cycle of more than a single year.

In my opinion the subterranean habit of the larvae may be an adaptation that protects them from the rapid temperature changes in the upper layers of the soil that occur at the high elevations where they live.

KEYS AND DIAGNOSES

Chiasognathini Felsche, 1889

Diagnosis.—All setae on the raster inclined laterally, never medially or erect (Fig. 44–49).

Key to Larvae of Genera of Chiasognathini

- 1. Antenna with subapical segment swollen distally with an acute projecting lobe, medial to which is a suboval sensory spot facing medially (Fig. 7); apical segment pyriform. Mesocoxa with pars stridens consisting of a single row of teeth expanded proximally into a field of teeth as wide as several teeth, each tooth subequal in size to those in the main row (Fig. 35). Metatrochanter with plectrum consisting of row of fewer than 48 teeth (Fig. 40) *Chiasognathus*

- 1'. Antenna with subapical segment distally rounded with sensory spot facing laterally (Fig. 6); apical segment subconical. Mesocoxa with pars stridens consisting of a single row of teeth, proximally with at most a patch of very small sparse granules (Fig. 36–39). Plectrum of metatrochanter consisting of row of more than 48 teeth (Fig. 41–43) *Sphaenognathus*

Genus *Chiasognathus* Stephens, 1831

I have seen larvae and associated adults of the following species: *Chiasognathus granti*, 1 male, Chile, Cayutue, Lago Todos Los Santos, Llanguihue, 14 October 1969, J. Solervinces A.; *Chiasognathus* sp., 1 female, Chile, Mañuales, L. Peña; *C. granti*, 14 larval skins, Chile, Lago Penihueico, Volcán Chosuencho, August 1988, O. Skew, ex boar stomach; *C. granti*, 2 males, XI Region, Coyhaique [no further data]. All specimens examined with mandibles worn; material deposited in QCAZ, CMNH, and CV.

Genus *Sphaenognathus* Buquet, 1838

Larva C-shaped, subcylindrical and thickened posteriorly (Fig. 1); mediolateral length, including head, 45–86 mm; color whitish blue when teneral and whitish yellow when fully developed.

Head capsule globose (Fig. 1–4), 8.0–11.6 mm wide, dark to light reddish brown with anterior pattern of clypeus yellowish brown; epicranial suture impressed, yellowish, approximately as long as frontal suture (epicranial suture appears shorter in Fig. 4 due to angle of view); surface of cranium bare to lightly punctate with 2–8 dorsoepicranial setae; stemma circular to ovate, not pigmented, without definite margin, not or slightly raised above head surface; frontal suture distinct, often asymmetrical; frons lightly punctate, becoming rugosopunctate anteriorly, with an ovate depression at top of epicranial suture corresponding to ocellar area; on each side, 1 or 2 setae at anterior angle, 1 or 2 exterior frontal setae, and 0 or 1 anterior frontal setae; clypeofrontal suture distinct, impressed. Clypeus trapezoidal, 3.0–3.7 times as long as wide, 1 or 2 anterior clypeal setae and 1 or 2 exterior clypeal setae on each side; preclypeus lightly sclerotized, rugosopunctate. Labrum suboval, rugosopunctate, wider than long, with 2 anterior labral setae, 10–20 posterior labral setae. Apex of epipharynx (Fig. 8, 9, 11–14), in frontal view, with 13–18 long, thick setae directed anteromedially; haptomerum with at least two truncate coarse heli; chaetopariae consisting of 18–93 long setae and numerous small setae directed medioapically; tormae united, laeotorma and dextortorma almost symmetrical; pterotormae symmetrical, with apex rounded, acute or broadly truncate; epitorma with rounded apex and deeply impressed in surface of pedium; haptolachus with three suboval nesia, the medial nesium sometimes hardly distinct from sclerotized sensory cone, the right nesium larger than left nesium; a patch of small setae on each side of sensory area. Mandibles subtriangular (Fig. 2, 15–23), asymmetrical, brownish; dorsa of mandibles (Fig. 16, 17, 19–23) with small dorsomolar setae on base of molar area, one large caudolateral seta at scissorial notch and one large lateral seta on molar area; ventral surface of mandibles (Fig. 15, 18) with patch of ventromolar setae and a patch of ventrolateral setae; basolateral angle with ventral subtriangular process; basolateral angle with rounded postartis; scissorial area of left mandible (Fig. 15, 16) with 4–5 teeth (unknown in *S. subtilis*), inner margin of left mandible between scissorial and molar areas with or without basal tooth (Fig. 15, 16, 19–23); teeth of molar area (Fig. 15, 16) not well-defined, with masticatory concave area projecting

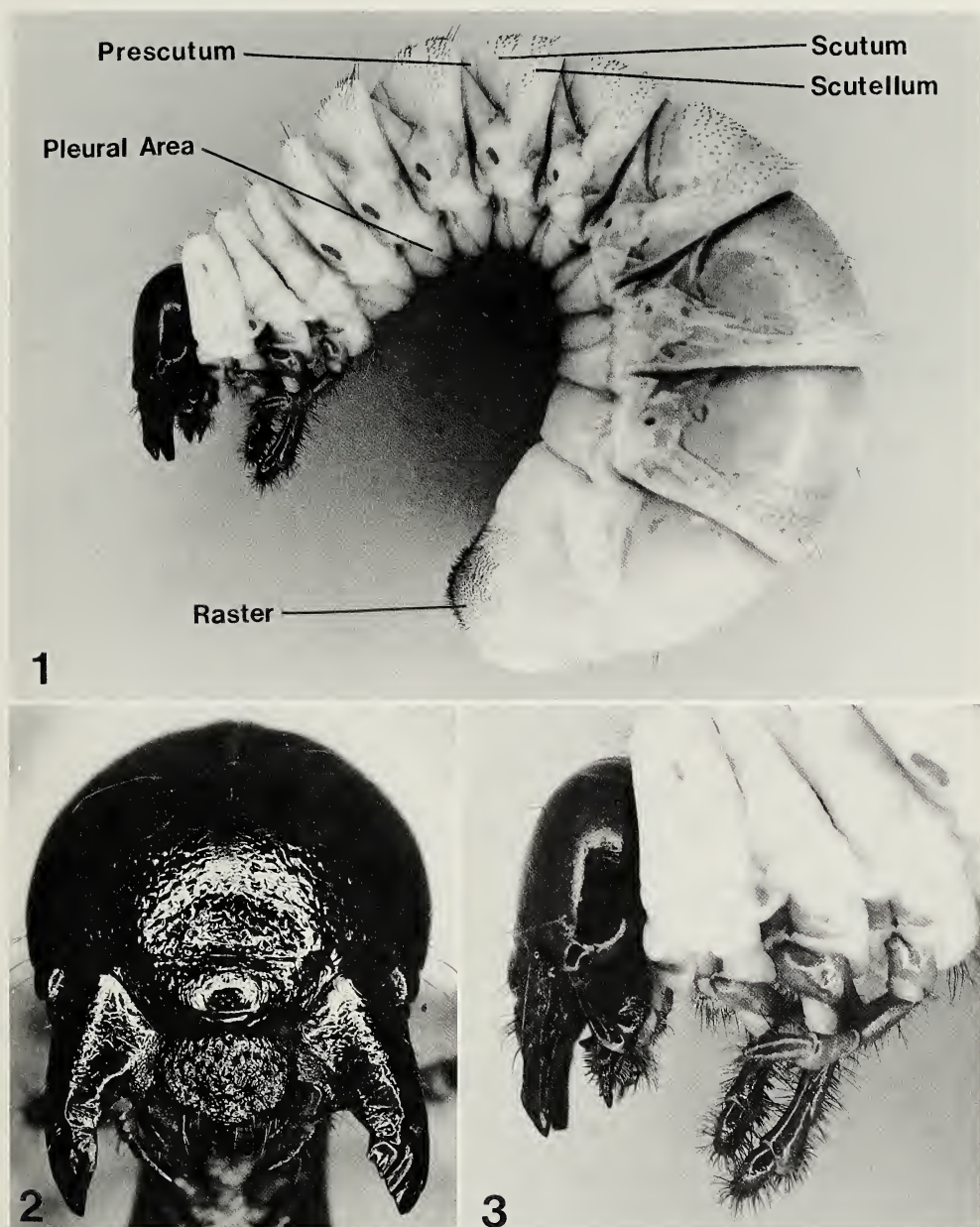


Fig. 1-3.—Third instar larva of *Sphaenognathus peruvianus*. 1, left lateral view; 2, head, frontal view; 3, head and thorax, left lateral view.

anteriorly and retracted posteriorly; acia present (Fig. 16); scissorial area of right mandible with teeth often not well-defined; molar area with masticatory area convex. Maxillae (Fig. 25, 26) each with galea and lacinia separate; galea with strong subconical uncus and 5-7 large setae lateral to uncus; lacinia with terminal subconical uncus, 10-17 large setae behind uncus; stipes with large strip of small

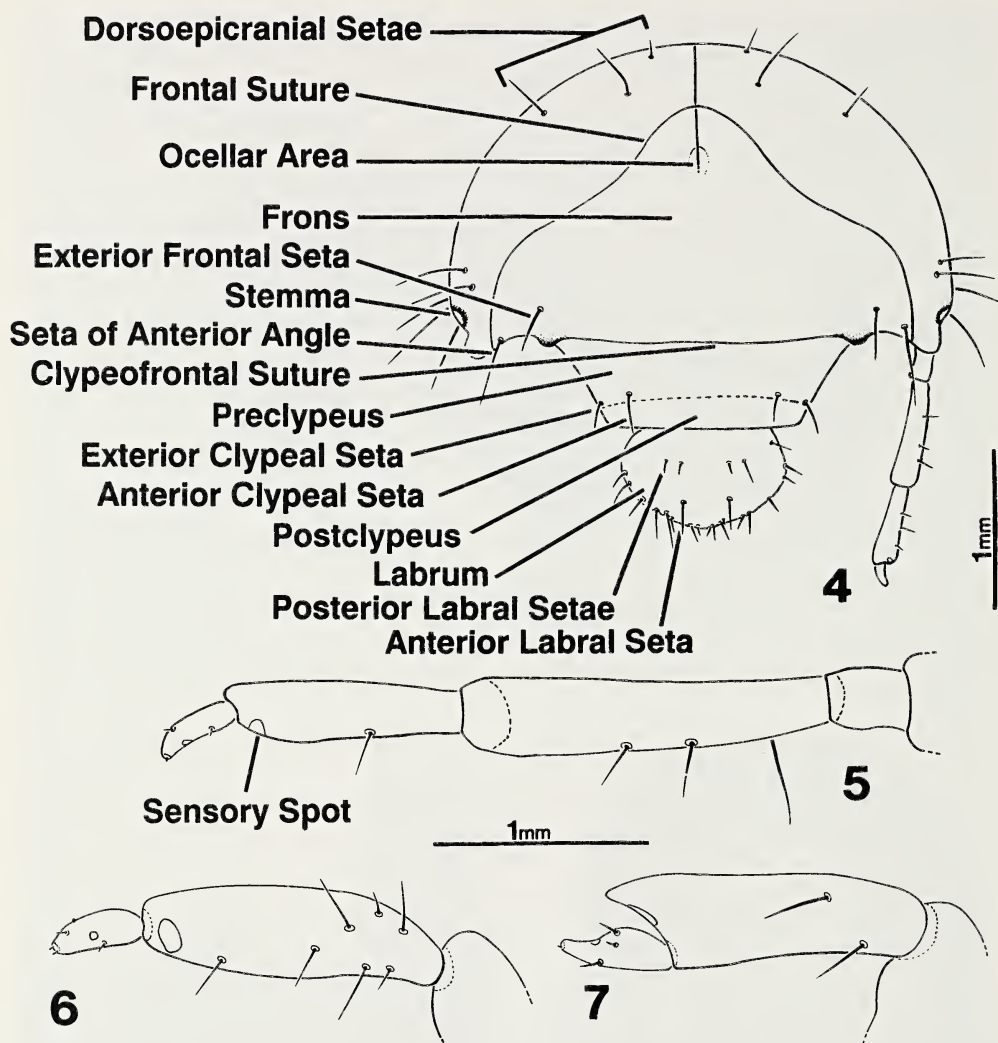


Fig. 4-7.—Third instar larvae of Chiasognathini. 4, *Sphaenognathus nobilis*, head; 5, *S. subtilis*, left antenna, dorsal view; 6, *S. oberon*, third and fourth antennomeres of right antenna, lateral view; 7, *Chiasognathus granti*, third and fourth antennomeres of right antenna, lateral view.

teeth set in a lightly sclerotized area; maxillary palpus with four palpomeres; basal palpomere as long as wide, with subcircular unpigmented area; second palpomere shorter than basal, subconical with subcircular unpigmented area; third palpomere subcylindrical, as long as second palpomere; apical palpomere subconical, longer than basal palpomere; palpomere 1-3 setose, apical palpomere glabrous. Labium (Fig. 24): labial palpi with two palpomeres, apical palpomere subconical, twice or more length of basal palpomere; hypopharyngeal sclerome heavily sclerotized, concave medially, asymmetrical; sublateral lobes of sclerome reduced to two unpigmented spots, the right spot smaller than left; sclerome with left side of anterior margin with strong conical teeth directed dorsally. Antennae (Fig. 4-6)

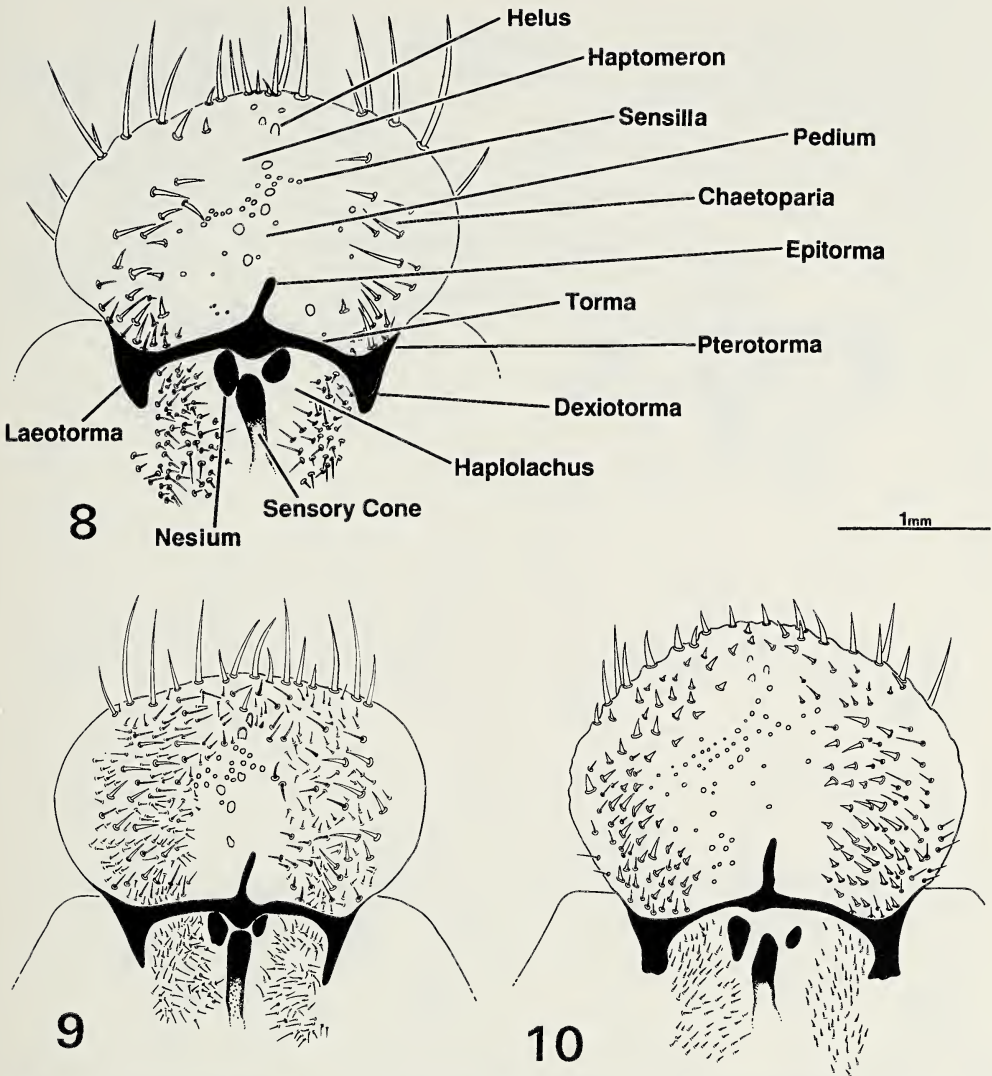


Fig. 8–10.—Epipharynges of third instar larvae of Chiasognathini. 8, *Sphaenognathus nobilis*; 9, *S. peruvianus*; 10, *Chiasognathus granti*.

geniculate, each with four antennomeres; basal antennomere subcylindrical, about as long as apical; second antennomere clavate, longer than third; third antennomere clavate with a subapical and externally directed sensory spot; fourth antennomere subconical, externally directed and with a sensory spot; second to fourth antennomeres setose.

Thorax (Fig. 3, 27) divided into prothorax, mesothorax, and metathorax; prothoracic dorsum with two narrow transverse rows of long setae, anterior row with many setae, posterior row with few setae; each side of prothorax with sclerotized furrow, continuous (Fig. 27) or interrupted below the middle (Fig. 3); mesothorax divided into two dorsal areas, posterior one with row of long setae; metathorax with dorsum similar to mesothorax; pleural area of mesothorax and metathorax

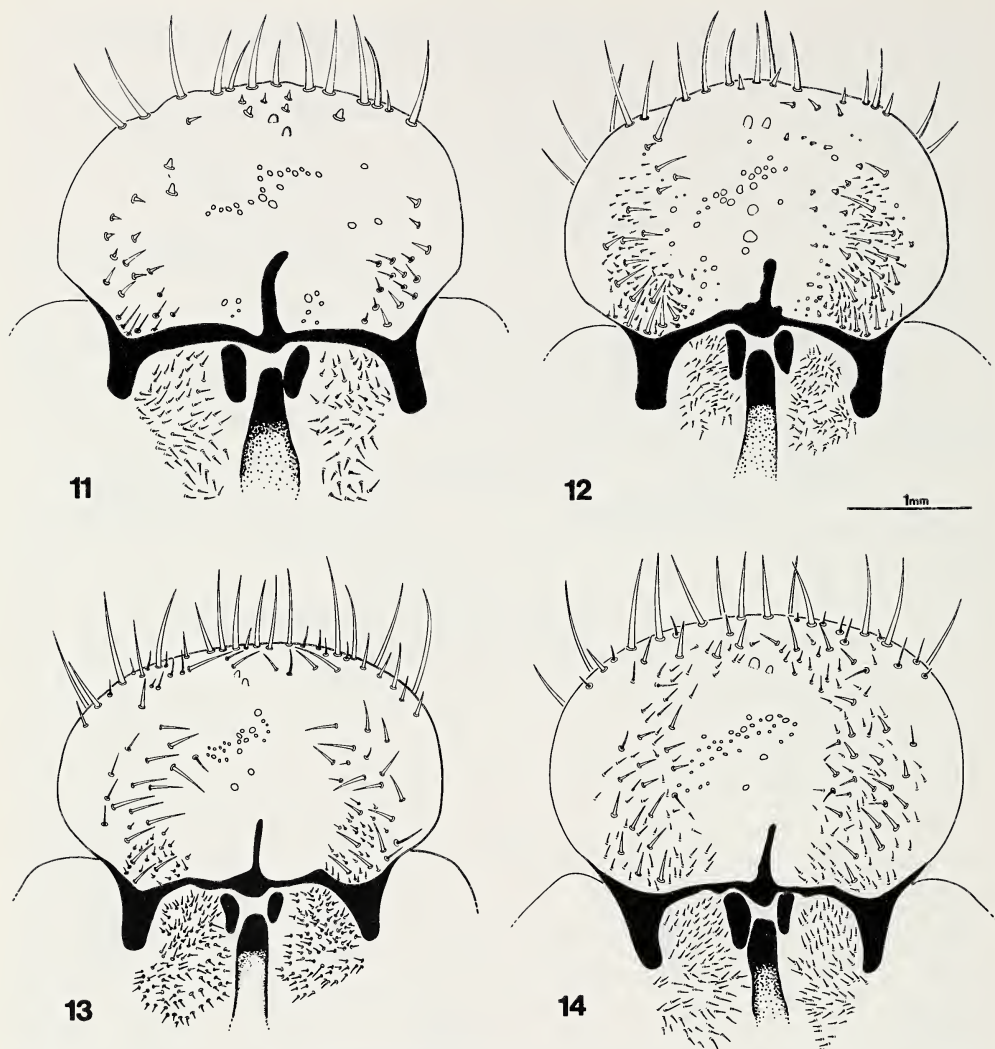


Fig. 11-14.—Epipharynxes of third instar larvae of *Sphaenognathus*. 11, *S. subtilis*; 12, *S. metallifer*; 13, *S. lindenii*; 14, *S. oberon*.

each with a tubercle with a patch of long setae. Prothoracic legs (Fig. 31) slightly shorter than mesothoracic and metathoracic legs (Fig. 33, 34); metathoracic legs directed anterolaterally and perpendicular to those of mesothorax and prothorax. Each leg with setose coxa, trochanter, femur, tibia, and tarsungulus (Fig. 31, 33, 34); tarsungulus abruptly attenuated at apex forming very short median tooth, flanked by two setae rising from same position on each side (Fig. 32); coxae of mesothoracic legs (Fig. 36-39) with a stridulatory area or pars stridens, consisting of a slightly curved, longitudinal row of subconical teeth raised into slight carina, lateral end of carina diffusing into small patch of granules, medial end with very small patch or no patch of granules; trochanter of each metathoracic leg (Fig. 41-43) with a stridulatory area or plectrum consisting of a single longitudinal row of

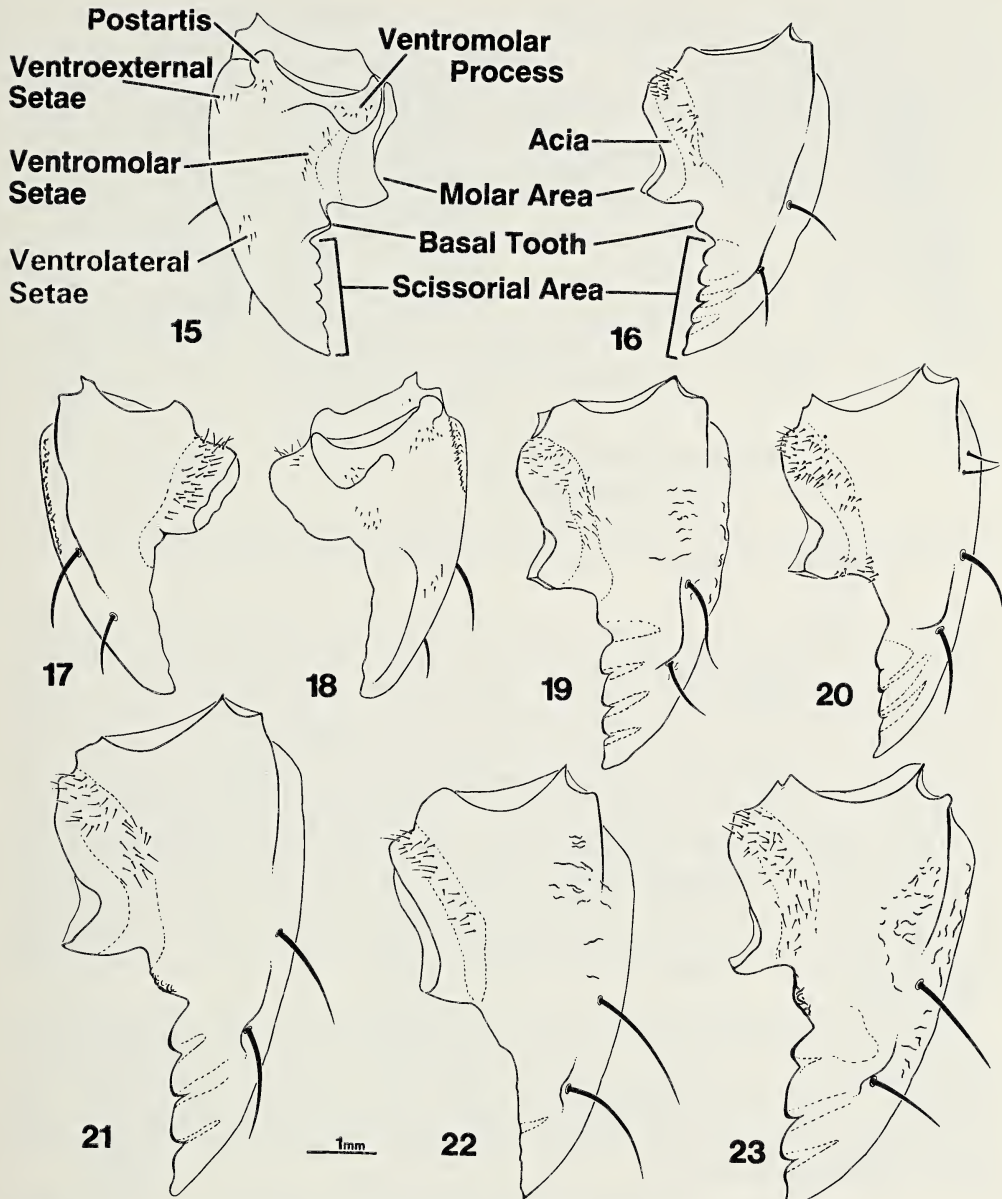


Fig. 15–23.—Mandibles of third instar larvae of *Sphaenognathus*. 15, *S. nobilis*, left mandible, ventral view; 16, *S. nobilis*, left mandible, dorsal view; 17, *S. nobilis*, right mandible, dorsal view; 18, *S. nobilis*, right mandible, dorsal view; 18, *S. nobilis*, right mandible, ventral view; 19, *S. metallifer*, left mandible, dorsal view, 20, *S. peruvianus*, left mandible, dorsal view; 21, *S. lindenii*, left mandible, dorsal view; 22, *S. subtilis*, left mandible, dorsal view; 23, *S. oberon*, left mandible, dorsal view.

short rounded, suboval or elongate teeth; teeth decreasing in size or becoming elongate distally; trochanter swollen apically with a moderate projecting lobe.

Abdominal terga 1–8 becoming longer posteriorly (Fig. 1); tergum 9 about same length as tergum 6; abdominal segment 1 with two dorsal areas, posterior area

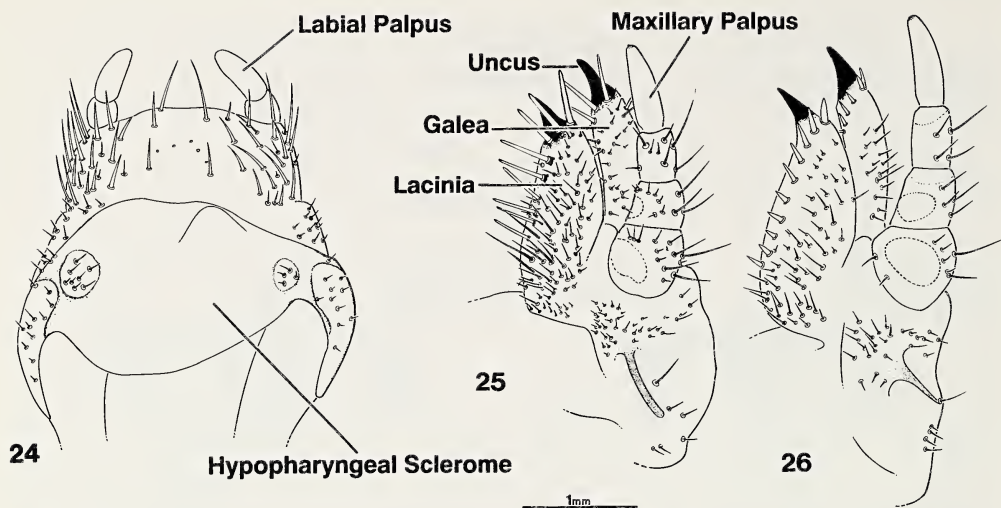


Fig. 24-26.—Mouthparts of third instar larvae of *Sphaenognathus*. 24, *S. subtilis*, labium, dorsal view; 25, *S. metallifer*, right maxilla, dorsal view; 26, *S. subtilis*, right maxilla, dorsal view.

with row of long setae; segments 2-6 with prescutum, scutum, and scutellum; scutum and scutellum divided by asperities; scutum covered by short thick setae; scutellum covered by short thick setae and posteriorly with transverse row of long setae; segments 7-9 with two dorsal areas, each with transverse row of long setae; segment 10 with one dorsal area with transverse row of long setae; pleural area of segments 1-9 each with prominent tubercle bearing patch of long setae; anal opening (Fig. 44-48) Y-shaped, stem of Y much longer than arms; upper anal lobe very small, insignificant; lateral lobe with kidney-shaped and glabrous pad; raster (Fig. 48) consisting of mixed short to long stout setae directed laterally; sternum 10 about two times as long as tergum 10; sternum 9 about half as long as tergum 9; Herold's organ on anal border of sternum 9 present in male (Fig. 49) and absent in female; sterna 1-8 bilobed, each with transverse row of long sparse setae.

Spiracles (Fig. 28-30) yellowish brown with cribriform respiratory plate; spiracles present on nine segments; respiratory plate of prothoracic spiracle kidney-shaped (Fig. 29) or C-shaped (Fig. 28) with concavity directed anteriorly with subcircular bulla; respiratory plate of abdominal spiracles C-shaped (Fig. 30) becoming smaller posteriorly; abdominal spiracle 5 subequal in size to respiratory plate of prothoracic spiracle.

Key to Known Larvae of *Sphaenognathus*

- 1'. Prothorax with lateral sclerotized furrow clearly interrupted by a non-sclerotized area (Fig. 3). Raster with more than 900 short to long setae (Fig. 1) *Sphaenognathus peruvianus*
- 1'. Prothorax with lateral sclerotized furrow continuous, not interrupted by a nonsclerotized area (Fig. 27). Raster with fewer than 900 short to long setae (Fig. 48) 2
- 2(1'). Anal lobes glabrous (Fig. 46) *Sphaenognathus subtilis*

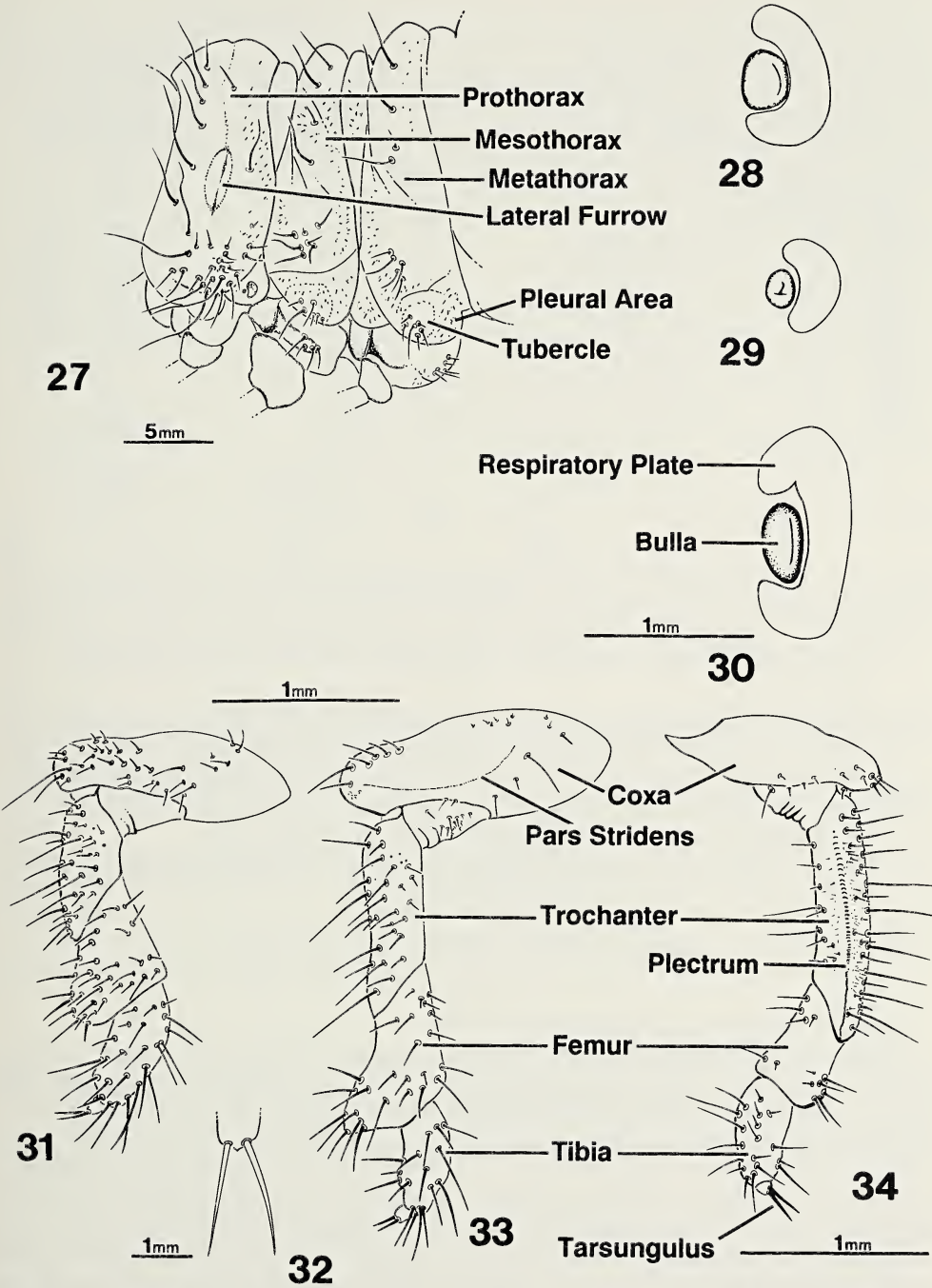


Fig. 27-34.—Third instar larvae of *Sphaenognathus*. 27, *S. nobilis*, thorax, left lateral view; 28, *S. subtilis*, left thoracic spiracle; 29, *S. nobilis*, left thoracic spiracle; 30, *S. nobilis*, left spiracle, abdominal segment 3; 31, *S. peruvianus*, right prothoracic leg; 32, *S. peruvianus*, tarsungulus of right prothoracic leg; 33, *S. metallifer*, left mesothoracic leg; 34, *S. peruvianus*, right metathoracic leg.

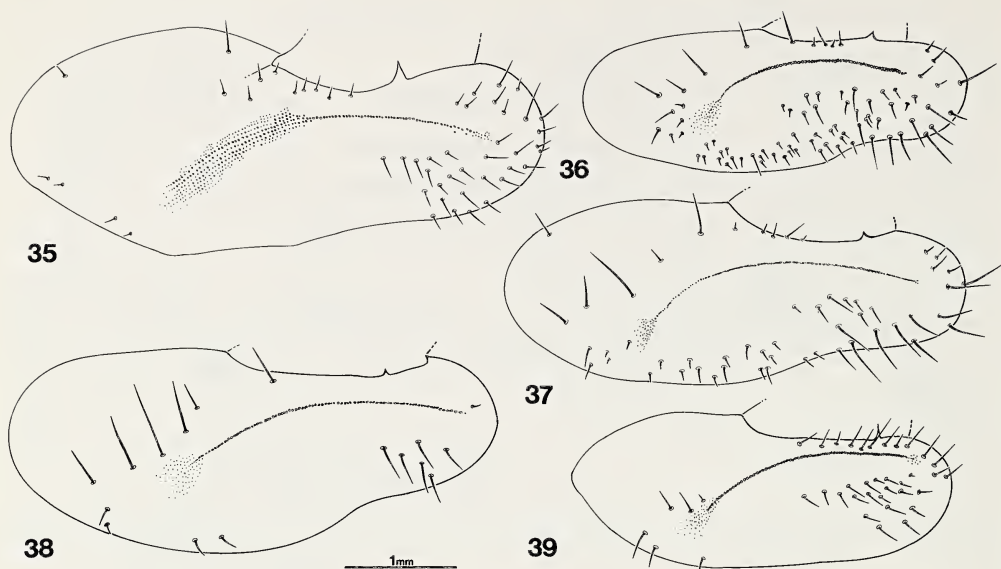


Fig. 35-39.—Pars stridens on coxa of left mesothoracic leg, third instar larvae of Chiasognathini. 35, *Chiasognathus grantii*; 36, *Sphaenognathus nobilis*; 37, *S. metallifer*; 38, *S. subtilis*; 39, *S. peruvianus*.

- 2'. Anal lobes densely tomentose (microsetae 0.02–0.12 mm long) (Fig. 44, 45, 47) 3
- 3(2'). Left mandible with five teeth in the scissorial area (Fig. 15, 16). Respiratory plate of thoracic spiracle kidney-shaped (Fig. 29) *Sphaenognathus nobilis*
- 3'. Left mandible with four teeth in the scissorial area (Fig. 19, 21, 23). Respiratory plate of thoracic spiracle C-shaped (Fig. 28) *Sphaenognathus lindenii*, *S. metallifer*, and *S. oberon*

DESCRIPTIONS

Sphaenognathus lindenii Murray, 1857

Larva

Mediolateral Length.—68–76 mm.

Head.—Width of cranium 9.3–11.6 mm; cranium surface dark reddish brown, yellowish spotted. Dorsoepicranial setae 2–5 on each side. Frons on each side with 1 or 2 setae at anterior frontal angle, 1 or 2 exterior frontal setae, and 0–1 anterior frontal setae. Clypeus trapezoidal with length 3.5–3.7 times width, with 1 or 2 anterior clypeal setae and 1 or 2 exterior clypeal setae on each side. Labrum with 10–15 posterior and two anterior labral setae. Epipharynx (Fig. 13): haptomerum with 2–3 heli; pedium with 24–27 sensilla; right chaetoparia with 10–15 long setae and some smaller setae; left chaetoparia with 10–24 long setae and some smaller setae; pterotormae subparallel and rounded apically. Left mandible with four blade-like scissorial teeth, basal tooth conical and dull (Fig. 21). Maxillae each with 5–6 large setae lateral to uncus of galea and 13–16 large setae behind uncus of lacinia.

Thorax.—Respiratory plate of thoracic spiracle C-shaped. Prothorax with sclerotized lateral area forming a long furrow. Each mesothoracic leg with pars stridens

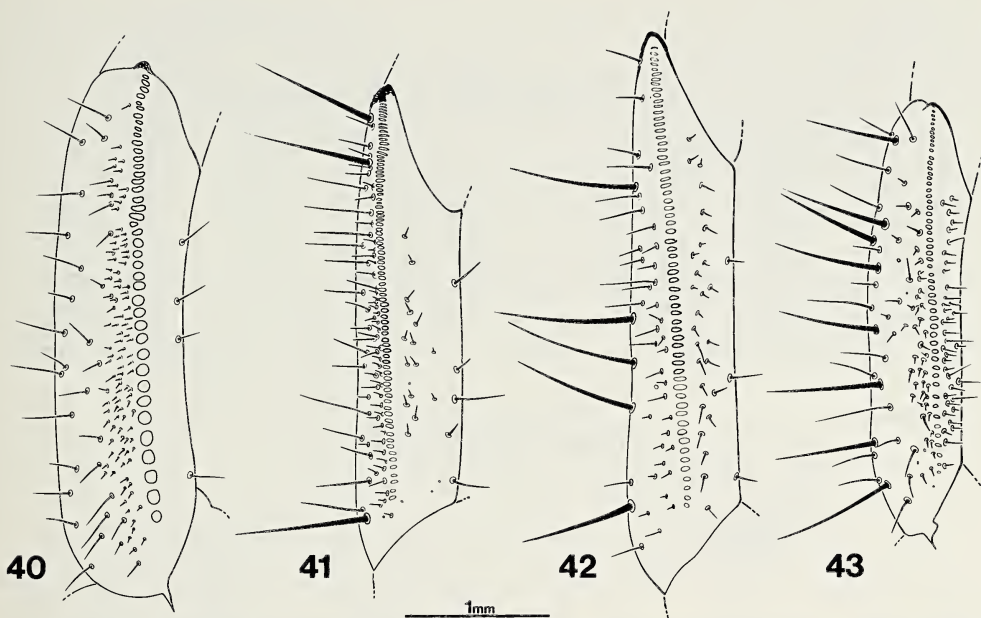


Fig. 40–43.—Plectrum on trochanter of right metathoracic leg, third instar larvae of Chiasognathini. 40, *Chiasognathus* sp.; 41, *Sphaenognathus metallifer*; 42, *S. subtilis*; 43, *S. nobilis*.

consisting of 92–108 teeth; metathoracic legs each with plectrum consisting of 83–105 suboval teeth, distal teeth becoming more elongate.

Abdomen.—Upper and lateral anal lobes covered by short thick setae 0.04–0.12 mm long; anal pad bare (Fig. 45). Raster consisting of 366–386 short to long setae.

Larval Material.—Description based on the following third instar larvae: five males and 14 females with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Pichincha, La Cocha, 3000 m, February to March 1989, G. Onore, 5–25 cm deep in sod soil.

Pupa

Male Pupa.—(Fig. 50–52). Shape elongate, exarate; length 43–54 mm; color yellowish brown, becoming greenish brown just prior to adult eclosion.

Head.—Ceratotheca elongate, with few short scattered setae. Ophthalmothecae distinctly visible with sclerotized lunate border anteriorly. Maxillary palpi distinct, longer than mandibles.

Thorax.—Podothecae with three segments discernible; metatarsi reaching the fifth abdominal segment. Pterothecae closely appressed and curving ventrally around body. Mesonotum and metanotum each with a prominent bump medio-posteriorly; pronotum subtrapezoidal, 1.75 times as wide as long, with two prominent bumps medioposteriorly; pronotum, mesonotum, and metanotum with few scattered, short setae.

Abdomen.—Abdominal sterna with small scattered setae; apical segment with genitalia distinctly visible between urogomphi; nine abdominal terga visible; terga 1–8 with a transverse row of small setae and at posterior border a transverse row

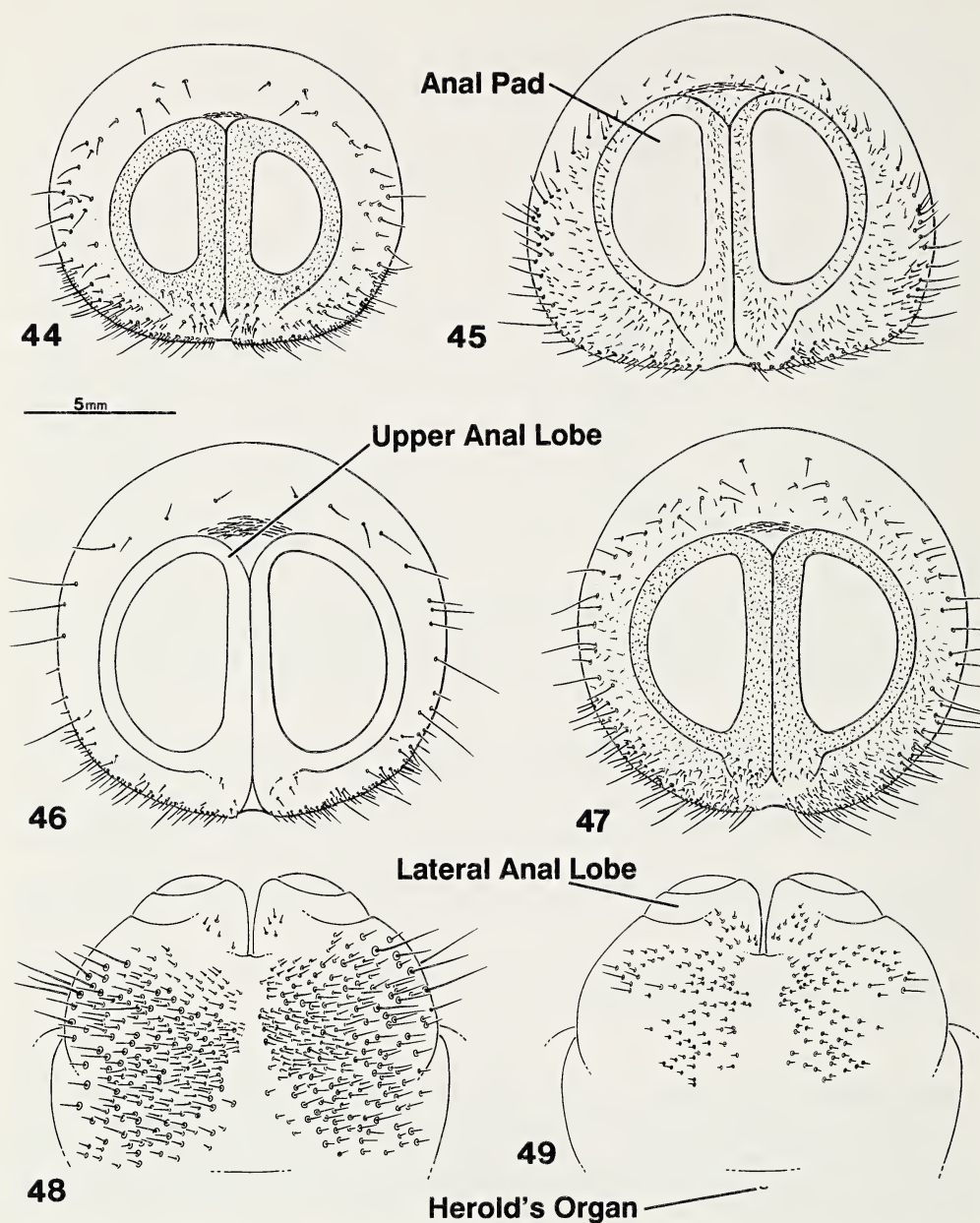


Fig. 44-49.—Posterior abdominal structures of Chiasognathini. 44, *Sphaenognathus nobilis*, caudal view of last abdominal segment; 45, *S. lindanii*, caudal view of last abdominal segment; 46, *S. subtilis*, caudal view of last abdominal segment; 47, *S. metallifer*, caudal view of last abdominal segment; 48, *S. subtilis*, sternum of last abdominal segment; 49, *Chiasognathus granti*, sterna 9-10 of male larva showing Herold's organ.

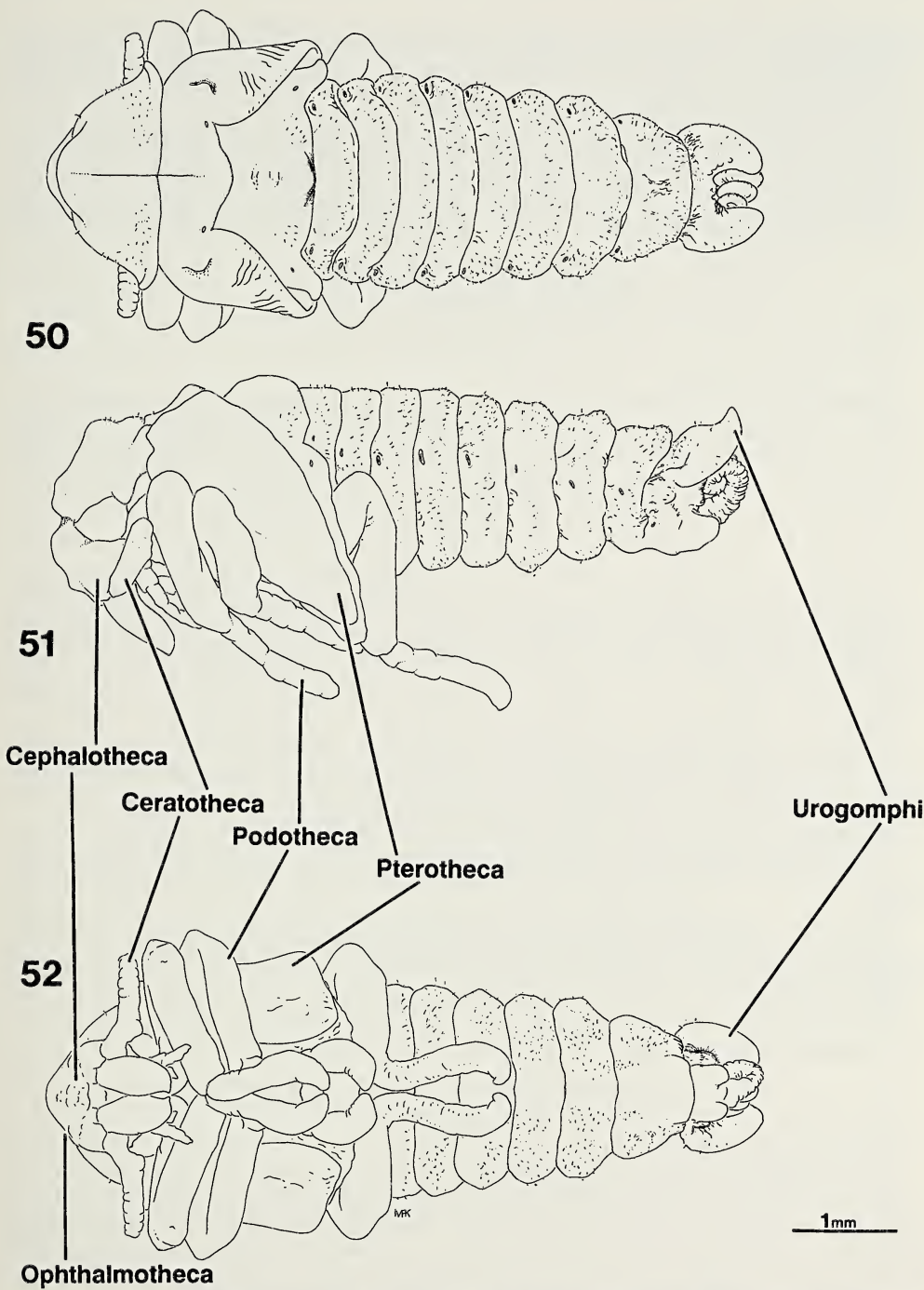


Fig. 50–52.—Pupa of *Sphaenognathus lindenii* (very fine setae on abdominal terga not shown). 50, dorsal view; 51, left lateral view; 52, ventral view.

of long setae (these setae not depicted in Fig. 50, 51). Abdominal spiracles eight on each side.

Female Pupa.—Length 52 mm. Similar to male except mandible shorter than in male and external genitalia very reduced.

Pupal Material.—Description based on the following pupae: four males and one female with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Pichincha, La Cocha, January 1988, G. Onore, 15–20 cm deep; in pupal cells, in sod soil; between roots of *Lachemilla orbiculata* (Rosaceae).

Sphaenognathus metallifer

Bomans and Lacroix, 1972

Larva

Mediolateral Length.—68–86 mm.

Head.—Width of cranium 8.8–10.1 mm; cranium surface dark reddish brown, yellowish spotted. Dorsoepicranial setae 2–4 on each side. Frons on each side with one seta at anterior frontal angle, one exterior frontal seta, and no anterior frontal seta. Clypeus trapezoidal with length 3.1–3.6 times width, with one anterior clypeal seta and one exterior clypeal seta on each side. Labrum with 15–20 posterior and two anterior labral setae. Epipharynx (Fig. 12): haptomerum with 2–5 heli; pedium with 28–50 sensilla; right chaetoparia with 17–26 long setae and some smaller setae; left chaetoparia with 20–27 long setae and some smaller setae; pterotormae subparallel and rounded apically. Left mandible with four blade-like scissorial teeth, basal tooth conical and dull (Fig. 19). Maxillae each with 5–7 large setae lateral to uncus of galea and 15–17 large setae behind uncus of lacinia (Fig. 25).

Thorax.—Respiratory plate of thoracic spiracle C-shaped. Prothorax with sclerotized lateral area forming a long furrow. Each mesothoracic leg with pars stridens (Fig. 37) consisting of 83–88 teeth; metathoracic legs each with plectrum (Fig. 41) consisting of 73–85 suboval teeth, distal teeth becoming more elongate.

Abdomen.—Upper and lateral anal lobes covered by short thick setae 0.04–0.12 mm long; anal pad bare (Fig. 47). Raster consisting of 462–464 short to long setae.

Material.—Description based on the following third instar larvae: six males and ten females with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Cañar, El Tambo, 2900 m, February 1990, G. Onore, 5–20 cm deep in grassy soil.

Sphaenognathus nobilis Parry, 1874

Larva

Mediolateral Length.—45–72 mm.

Head.—Width of cranium 8.0–9.1 mm; cranium surface dark reddish brown, yellowish spotted. Dorsoepicranial setae 2–3 on each side (Fig. 4). Frons on each side with one seta at anterior frontal angle, one exterior frontal seta, and no anterior frontal setae. Clypeus trapezoidal with length 3.10–3.14 times width, with one anterior clypeal seta and one exterior clypeal seta on each side. Labrum with 8–12 posterior labral seta and two anterior labral setae. Epipharynx (Fig. 8): haptomerum with 2–4 heli; pedium with 23–31 sensilla; right chaetoparia with 15–16 long and some smaller setae; left chaetoparia with 13–18 long and some smaller setae; pterotormae rounded apically and internally directed. Left mandible with

five blade-like scissorial teeth, basal tooth conical and dull (Fig. 15, 16). Right mandible in dorsal view (Fig. 17) and in ventral view (Fig. 18) with teeth not well-defined. Maxillae each with 4–6 large setae lateral to uncus of galea and 15–17 large setae behind uncus of lacinia.

Thorax.—Respiratory plate of thoracic spiracle kidney-shaped (Fig. 27, 29). Prothorax with sclerotized lateral area forming a long furrow (Fig. 27). Each mesothoracic leg with pars stridens consisting of 83–86 teeth (Fig. 36); metathoracic legs each with plectrum consisting of 50–57 suboval teeth (Fig. 43).

Abdomen.—Upper and lateral anal lobes covered by short setae 0.02–0.07 mm long; anal pad bare (Fig. 44). Raster with 586–730 short to long setae.

Material.—Description based on the following third instar larvae: five males and 13 females with associated adults; deposited in IZAV, QCAZ, and CMNH collections.

Locality.—Venezuela: Merida, La Mucuy, 2700 m, 18 Apr 1989, G. Onore and C. Bordon. In topsoil 3–15 cm deep, between roots of cultivated *Cupressus macrocarpa* (Cupressaceae) and native *Podocarpus rospigliosi* (Podocarpaceae).

Sphaenognathus oberon Kriesche, 1922

Larva

Mediolateral Length.—62–86 mm.

Head.—Width of cranium 10.0–10.6 mm; cranium surface dark reddish brown, yellowish spotted. Dorsoepicranial setae 2–4 on each side. Frons on each side with 1 or 2 setae at anterior frontal angle, 1 or 2 exterior frontal setae, and no anterior frontal setae. Clypeus trapezoidal with length 3.6–3.7 times width, with one anterior clypeal seta and one exterior clypeal seta on each side. Labrum with 10–15 posterior labral setae and two anterior labral setae. Epipharynx (Fig. 14): haptomerum with 2–4 heli; pedium with 28–64 sensilla; right chaetoparia with 16–25 long setae and some smaller setae; left chaetoparia with 23–30 long setae and some smaller setae; pterotormae subparallel and rounded apically. Left mandible with four scissorial teeth blade-like, basal tooth conical and dull (Fig. 23). Maxillae each with 5–7 large setae lateral to uncus of galea and 10–17 large setae behind uncus of lacinia. Apical antennomere subconical (Fig. 6).

Thorax.—Respiratory plate of thoracic spiracle C-shaped. Prothorax with sclerotized lateral area forming a long furrow. Each mesothoracic leg with pars stridens consisting of 85–87 teeth; metathoracic legs each with plectrum consisting of 60–83 suboval teeth, distal teeth becoming more elongate.

Abdomen.—Upper and lateral anal lobes covered by short thick setae 0.5–0.12 mm long; anal pad bare. Raster with 412–508 small to long setae.

Material.—Description based on the following third instar larvae: seven males, three females, and three larvae of undetermined sex with damaged genital regions, all with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Bolivar, Santiago, Casha Totoras, 2900 m, March 1989, G. Onore, 10–25 cm deep in the soil covered by cultivated *Solanum tuberosum* (Solanaceae).

Sphaenognathus peruvianus (Waterhouse, 1869)

Larva

Mediolateral Length.—58–76 mm (Fig. 1).

Head.—Width of cranium 8.0–10.0 mm; cranium surface reddish brown, yellowish spotted (Fig. 2, 3), 3–8 dorsoepicranial setae on each side. Frons on each

side with one or two setae at anterior frontal angle, one or two exterior frontal setae, and 0–1 anterior frontal setae. Clypeus trapezoidal with length 3.4 times width, with one anterior clypeal seta and one or two exterior clypeal setae on each side. Labrum with 19 posterior labral setae and two anterior labral setae. Epipharynx (Fig. 9): haptomerum with two heli; pedium with 21–29 sensilla; right chaetoparia with 30–41 long and some smaller setae; left chaetoparia with 30–52 long and some smaller setae; pterotormae subtriangular and slightly internally directed. Left mandible with four blade-like scissorial teeth and without basal tooth (Fig. 2, 20). Maxillae each with five large setae lateral to uncus of galea and 15–16 large setae behind uncus of lacinia.

Thorax.—Respiratory plate of thoracic spiracle C-shaped (Fig. 3). Prothorax with sclerotized lateral area consisting of furrow interrupted by a nonsclerotized area, the part of furrow ventral to interruption shorter than dorsal (Fig. 3). Prothoracic leg (Fig. 31). Each mesothoracic leg with pars stridens (Fig. 39) consisting of 79–88 teeth; metathoracic legs each with plectrum (Fig. 34) consisting of 66–82 conical teeth, distal teeth becoming more elongate. Tarsungulus of prothoracic, mesothoracic, and metathoracic legs (Fig. 32).

Abdomen.—Upper and lateral anal lobes covered by very sparse, scattered short setae 0.02–0.06 mm long; anal pad bare. Raster with 940–990 short to long setae.

Material.—Description based on the following third instar larvae: seven males and seven females with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Loja, 4°16'S, 79°20'W, 2800 m, 24 March 1990, G. Onore, 5–15 cm in topsoil.

Sphaenognathus subtilis Lacroix, 1987

Larva

Mediolateral Length.—81 mm.

Head.—Width of cranium 10.8 mm; cranium surface dark reddish brown. One dorsoepicranial seta on each side. Frons on each side with one seta at anterior frontal angle, one exterior frontal seta, and no anterior frontal seta. Clypeus trapezoidal with length 3.2 times width, with one anterior clypeal seta on each side; one exterior clypeal seta on the left side and two setae on the right side. Epipharynx (Fig. 11): haptomerum with two heli; pedium with 50 sensilla; right chaetoparia with 12 long setae and some smaller setae; left chaetoparia with six long setae and some smaller setae, pterotormae rounded apically. Left mandible with scissorial teeth and the inner margin of the scissorial area worn (Fig. 22). Maxillae (Fig. 26) each with 6–7 large setae lateral to uncus of galea and 12–17 large setae behind uncus of lacinia. Labium (Fig. 24). Antenna (Fig. 5).

Thorax.—Respiratory plate of thoracic spiracle C-shaped (Fig. 28). Prothorax with sclerotized lateral area forming a long furrow. Each mesothoracic leg with pars stridens (Fig. 38) consisting of 84 teeth; metathoracic legs each with plectrum (Fig. 42) consisting of 62 suboval teeth, distal teeth becoming elongate.

Abdomen.—Anal lobes and anal pad bare (Fig. 46). Raster (Fig. 48) with about 324 small to long setae.

Material.—Description based on one female third instar larva, fully developed, associated with adults; deposited in CMNH collection.

Locality.—Ecuador: Napo, Cosanga, 1500 m, G. Onore. Under rotten log in grass-covered soil.

DISCUSSION

For this study I examined larvae of the following genera: *Ceratognathus*, *Ceruchus*, *Chiasognathus*, *Dorcus*, *Figulus*, *Lamprima*, *Lissapterus*, *Lissotes*, *Lucanus*, *Platycerus*, *Sinodendron*, *Sphaenognathus*, *Syndesus*, and *Rhyssonotus*. I assessed the characters of *Pholidotus* from the description and illustrations of Costa et al. (1988). The characters discussed below indicate that the genera most closely related to *Chiasognathus* and *Sphaenognathus* are *Rhyssonotus* and *Pholidotus*, and only these genera are discussed further. The same relationships were found by Lacroix (1969) and Holloway (1960) in their phylogenetic interpretations based on adults.

The following larval characters have been considered useful in distinguishing various groups of Lucanidae.

1. *Mandible*. The number of teeth in the left mandible has been used for distinguishing higher taxa of Lucanidae (Van Emden, 1935, 1941; Ritcher, 1966; Lawrence, 1981). However, this character is a problem to assess in larvae that have not recently molted, due to normal wear of the mandibles. The teeth are divided into two categories: the teeth of the scissorial area and the teeth basal to the scissorial area (between the scissorial area and the molar area) which I here designate "basal teeth" (Fig. 15, 16). The mandibles in *S. lindenii*, *S. metallifer* (Fig. 19), and *S. oberon* have four scissorial teeth; the same condition is found in *Rhyssonotus* sp. Costa et al. (1988) illustrated four scissorial teeth in *Pholidotus spixi*. *Sphaenognathus nobilis* has five scissorial teeth (Fig. 15, 16), and the condition is unknown in *S. subtilis* and *Chiasognathus granti*. Two basal teeth are present in *Rhyssonotus*, and one basal tooth in *S. lindenii*, *S. oberon*, *S. metallifer*, and *S. nobilis* (Fig. 15, 16, 19, 21, 23). Basal teeth are absent in *S. peruvianus* (Fig. 20). This absence is interpreted as derived, and strengthens the reestablishment by Bartolozzi et al. (1992) of *Chiasognathinus* (Didier and Séguy, 1953) as a distinctive and perhaps monophyletic subgenus of *Sphaenognathus* containing *S. peruvianus* and *S. gaujoni* (Oberthür).

2. *Prothorax*. A sclerotized, anteriorly projecting lobe on the prothorax was used as a character by Ritcher (1966) and Lawrence (1981). This structure is not present in *Chiasognathus* and *Sphaenognathus*. A second character, the lateral sclerotized furrow (Fig. 1, 27), is continuous in all known larvae of *Sphaenognathus* except *S. peruvianus* wherein the furrow is interrupted by a nonsclerotized area. The latter condition is considered derived, and occurs as well in *Rhyssonotus*. The character was not illustrated for *Pholidotus* by Costa et al. (1988).

3. *Mesothoracic legs*. The shape, number and position of teeth of the pars stridens of the mesocoxae have been used by Van Emden (1952), Ritcher (1966), Klausnitzer (1978), and Lawrence (1981). Larvae of species of *Sphaenognathus* have similar structures except for the number of teeth (Fig. 36–39). The same condition is present in *Pholidotus* and *Rhyssonotus*. *Chiasognathus* larvae differ in having a distinctive field of teeth at the proximal end of the main row of teeth on the pars stridens (Fig. 35).

4. *Metathoracic legs*. The plectrum of the metatrochanter is functionally related to the pars stridens. In the genera *Sphaenognathus* (Fig. 41–43), *Chiasognathus* (Fig. 40), *Pholidotus*, and *Rhyssonotus*, this structure is very similar with variation only in the number and shape of the teeth.

5. *Setation of anal sclerite*. The dense vestiture of setae in the area surrounding the anal pad separates *S. lindenii*, *S. metallifer*, *S. oberon*, and *S. nobilis* (Fig. 44, 45, 47) from *S. peruvianus* and *S. subtilis* (Fig. 46), which lack this vestiture.

Chiasognathus, *Rhyssonotus*, and *Pholidotus* have a reduced number of dense setae.

6. *Epipharynx*. The basic anatomy of the epipharynx is similar in *Sphaenognathus* (Fig. 9, 11–14), *Chiasognathus* (Fig. 10), *Pholidotus*, and *Rhyssonotus*. Perhaps the most important character common to the above-mentioned genera is the vestiture of setae lateral to the nesia of the haptolachus. In *Chiasognathini*, the sensilla in the pedium and the setae of the paria seem to have the same origins and they are sometimes represented as “emerging setae”; in the haptomerum there are two or more coarse nail-like spines which I interpret as heli following Böving (1936).

7. *Tarsungulus*. Van Emden (1941), Medvedev (1952), Paulian (1959), and Ritcher (1966) used the number of setae present on the tarsungulus as a character separating Lucaninae from Dorcinae and some other subfamilies. *Sphaenognathus* (Fig. 32), *Chiasognathus*, *Pholidotus* and *Rhyssonotus* have two setae on the tarsungulus. This character indicates that they should be included in Dorcinae. However, other characters support a relationship with Lucaninae.

8. *Raster*. The setae of the raster, localized in patches, are all inclined laterally in species of *Chiasognathini* (Fig. 1, 44–49).

A larval diagnosis for the family Lucanidae remains speculative with so few larvae available for study. Larval features suggest that *Chiasognathini* is related to Lucaninae and Dorcinae in agreement with Holloway's analysis of adults. That author concludes, “There appears to be no valid reason, at the present time, for recognizing as distinct groups the . . . *Chiasognathinae*, *Dorcinae* . . . ; probably all . . . belong in *Lucaninae*” (Holloway, 1960).

The most recent larval keys to lucanid subfamilies, based primarily on Palearctic and Nearctic genera, will not place all *Chiasognathini* in Lucaninae because *S. peruvianus* lacks the tooth between the inner margin of the scissorial area and the molar area (Fig. 20), a character considered diagnostic for Lucaninae. An important character linking *Chiasognathini* to Lucaninae is the length of the dorsal surface of abdominal segment 10, being half or less the length of the ventral surface of that segment (Fig. 1).

Known larvae of *Sphaenognathus* are very similar in anatomy with the exception of *S. peruvianus*, which presents features distinctive enough to justify revaluation of the subgenus *Chiasognathinus*.

PHYLOGENETIC NOTES

Although characters of larvae do not permit complete resolution of the phylogeny of the species described here, several apomorphic characters support the monophyly of three taxa as follows.

1. The monophyly of a lineage consisting of all examined species of *Chiasognathini* is supported by four characters tentatively considered to be apomorphic. *Chiasognathini* is also characterized by the presence of larval stemmata, but this is plesiomorphic and not phylogenetically informative.

- a. All setae on the raster inclined or directed laterally. Other Scarabaeoidea have the setae uniformly directed medially or in many different directions.
- b. Reduction in size of the third anal lobe. The third lobe is not reduced in *Syndesus* and other Scarabaeoidea.
- c. Presence of a basal tooth on the scissorial margin of the mandible. This is also present in Lucaninae, although absent in other Scarabaeoidea. Its

absence in *Sphaenognathus peruvianus* is hypothesized to represent a secondary loss.

- d. Presence of short thick setae on the anal lobes. Such short thick setae are absent in *Syndesus*, but their occurrence in other Lucanidae is not known. They appear to have been secondarily lost in *Sphaenognathus subtilis*.

2. *Chiasognathus* shares three characters with *Syndesus* that may be considered plesiomorphic for Chiasognathini. The derived condition of each of these characters may represent synapomorphies for *Sphaenognathus* as here delimited.

- a. Teeth on the pars stridens in a single row. The pars stridens consists of a field of multiple, scattered teeth in *Chiasognathus* and *Syndesus*.
- b. Apex of penultimate antennomere not extended past the base of apical antennomere. In *Chiasognathus* and *Syndesus* the distal end of the penultimate antennomere is modified, and the unmodified condition in *Sphaenognathus* is interpreted as a secondary apomorphic reduction.
- c. Apical antennomere oblate to cylindrical. This antennomere is pyriform or conical in *Chiasognathus* and *Syndesus*.

3. The monophyly of a group consisting of *Sphaenognathus lindenii*, *S. oregon*, and *S. metallifer* is supported by one synapomorphy.

- a. Presence of minute, slender setae on the anal lobe. These tiny setae are absent in other Chiasognathini, *Syndesus*, and many other genera of Lucanidae.

Alterations in the existing classification of Chiasognathini based on the above characters would be premature, and must wait until a more extensive analysis of characters from all development stages has been completed.

ACKNOWLEDGMENTS

This research was conducted with support and facilities from the International Visitors Program at Carnegie Museum of Natural History, for which I thank Director J. E. King. I thank L. Arcos Terán and T. De Vries for support from the Departamento de Biología de la Pontificia Universidad Católica del Ecuador.

I am grateful to the institutions and persons providing specimens for study: OSUO, A. Asquith; FSCA, D. H. Habeck; QCAZ, L. Arcos; WSUC, R. S. Zack, Jr.; and C. Vergara. I thank the following persons for donating or exchanging specimens: J. F. Lawrence (CSIRO, Canberra, Australia); H. F. and A. T. Howden (Carleton University, Ottawa, Canada); and L. E. Peña G., J. Numhauser T., and J. Solervincas A. (all of Santiago, Chile). Field assistance was provided by L. A. Coloma (Departamento de Biología, Pontificia Universidad Católica del Ecuador) and C. Bordon (Maracay, Venezuela). I am grateful to H. F. Howden (Carleton University, Canada), D. W. Roubik (Smithsonian Tropical Research Institute, Panama), and R. E. Woodruff (Bureau of Entomology, Division of Plant Industry, Gainesville, Florida) for valuable suggestions and encouragement.

Adult Lucanidae associated with larvae were determined by L. Bartolozzi (Università degli Studi di Firenze, Firenze, Italy). J. Auber (Université Pierre et Marie Curie, Paris, France) kindly examined specimens to confirm the presence of the stemmata. L. Baert (Institut Royal des Sciences Naturelles, Bruxelles, Belgium) provided some rare publications on lucanid larvae. S. Thompson (Section of Botany, CMNH) assisted with botanical details.

Assistance with illustration was provided by C. W. Young (CMNH); M. A. Klinger (CMNH) rendered Fig. 50–52; M. A. Daman assisted with manuscript preparation. Two anonymous reviewers provided useful and constructive criticism. Finally, my special thanks to R. Davidson and J. E. Rawlins (CMNH) for friendly help, scientific advice, and endless patience in revising this paper.

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REVIEWS

THE SCENT OF ORCHIDS: OLFACTORY AND CHEMICAL INVESTIGATIONS. Roman Kaiser. 1993. Elsevier Science Publishers B.V., Amsterdam, The Netherlands. 259 pp., with charts, tables, line drawings, color photographs and index. ISBN 0-444-89841-7. \$175.00.

The Scent of Orchids is an expensive volume which, according to the publishers, is intended to convey the enormous variation in scent and appearance of orchid flowers to people engaged in the fragrance field, professional scientists, naturalists, and hobbyists. Many writers have reported on these variations, but the detailed analyses of the aroma chemistry of a large number of orchid species from five different geographic areas provided in this work are an innovation.

Roman Kaiser, a Swiss research chemist, photographer, and student of botany has, over the past ten years, documented more than 2000 orchid species employing olfactory descriptions and photographs. His treatise, divided into three parts and an appendix, incorporates many of the results of his investigations.

Kaiser's work provides an insight into the large number of odors produced by orchids which can be detected by vertebrate and insect pollinators, describes methods by which these scents may be collected and analyzed, tabulates the chemical composition of the scents of 155 orchid species, and provides a substantial reference list of orchid fragrance studies.

Part One, Introduction to the World of Orchid Scents, contains a brief history of the early study and appreciation of orchids, their habitats and geographical distribution, and a general description of an orchid's floral structure. This is followed by a section discussing the nature of plant scents, their toxicity to and storage by plants, and the importance of their volatility. Many readers may be surprised to learn that the scent given off by a plant is controlled by the plant's biological clock and is not dependent upon visible external stimuli. In addition to describing the principal methods of plant pollination in which scent is a factor, Kaiser provides a brief résumé of human efforts to utilize scented plant oils first for rituals and subsequently for medicinal and cosmetic purposes.

Of particular interest to scientists involved in the investigation of floral fragrances is the section devoted to a description of the author's techniques for trapping scents without damage to plants or flowers. Kaiser describes procedures for recovering aroma samples in the range of 1–300 μg and determining their qualitative and quantitative compositions by gas chromatography and mass spectrometry. A section on principles of orchid pollination and the part played by plant fragrances presents little new information but might be useful to readers unfamiliar with these topics.

Finally, in a section on the verbal description of scents, Kaiser emphasizes the importance of discrete recounting of smells to complement the complex analytical systems or as a substitute when the latter cannot identify all olfactory components of a fragrance. He borrows from perfumery four floral-scent groups identified both as to olfactory response and chemical composition and relates these more familiar flower fragrances to some specific orchid scents. The general orchidist will find the floral-image scent groups useful to describe the complex olfactory scent of

some orchid species. Orchid taxonomists may be disappointed that the author did not discuss utilization of scent composition patterns for orchid species identification, but his work demonstrates that both the quantitative and the qualitative composition of scent within a species can vary from plant to plant, and is also dependent upon plant maturity and the hour when a sample is collected.

Part Two, Interdisciplinary Discussion of Orchid Scents, describes floral scents of 146 selected species, representing approximately 10% of all orchid genera, conveniently arranged according to their country of origin into four geographic regions (American tropics, African tropics, Indo-Australian tropics and subtropics, and Europe). This section provides descriptions of habitats, scent chemistry, and scent release patterns, as well as high-quality, close-up color photographs of more than 140 orchid species, some seldom illustrated. Although these photographs will prove attractive to any orchidist, the orchid grower primarily interested in illustrations of orchid species should consider one of the many less expensive books of orchid illustrations as an alternative.

Part Three, The Chemistry of Orchid Scents, includes remarks on previous investigations of orchid fragrances, limitations of the present study, and some generalizations that can be drawn from the investigations described in earlier parts of the volume. Detailed specifications of the equipment used in the study are provided as well as characterizations of the analytical samples for which aroma chemistry is recorded. This is followed by tables displaying the chemical composition of the scents collected from orchid species described in Part Two.

The Appendix includes a list of 74 references worldwide to studies of floral fragrances of Orchidaceae and other plant families and, following this, a list of 36 books and journals for further reading about orchids.

The care with which the translation of the original text from German into English has been made provides comfortable reading. Throughout Parts One and Two, geometric diagrams are included to illustrate the molecular structure of principal components of fragrances of some orchid species. Unfortunately, there is neither a guide to the nonchemist for interpreting these diagrams nor an explanation of their significance. Even those comfortable with the diagrams will find the lack of captions inconvenient; the reference numbers of the diagrams appear in the text, but not always on the same page with the diagram. This book will be a useful reference for the investigator of floral fragrances, but probably is not a useful purchase, given its cost, for the much wider audience of amateur and professional botanists.

FREDRICK W. WRIGHT, JR., *Volunteer, Section of Botany.*

ERRATUM

Volume 62, number 3, page 248, line 4. It should read: Superdivision Neodiapsida
incertae sedis.

INSTRUCTIONS FOR AUTHORS

ANNALS OF CARNEGIE MUSEUM consist of contributions to the earth sciences, life sciences and anthropology, in 30 by 46 picas format (127 by 195 mm or 5 by 7½ inches). Submit all manuscripts to the Office of Scientific Publications. Authors should give particular attention to scientific content, format, and general style for the ANNALS. **Manuscripts that do not conform to the style of the ANNALS will be returned to the author immediately.** Every manuscript will be peer reviewed by at least two outside persons. Authors will be asked to subsidize, if funds are available, any or all costs of publication (approximately \$100/page printed).

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ANNALS of CARNEGIE MUSEUM

THE CARNEGIE MUSEUM OF NATURAL HISTORY

4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 63

31 MAY 1994

NUMBER 2

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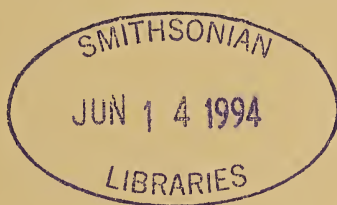
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ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

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PALAEOPHICHTHYS PARVULUS EASTMAN, 1908,
A GNATHORHIZID DIPNOAN FROM THE MIDDLE
PENNSYLVANIAN OF ILLINOIS, USA

HANS-PETER SCHULTZE¹

ABSTRACT

Palaeophichthys Eastman, 1908 is a gnathorhizid dipnoan. *Monongahela* Lund, 1970, a taxon based on isolated tooth plates, is its junior synonym. *Palaeophichthys* has tooth plates and a shoulder girdle typical of a gnathorhizid. The genus is distinct from *Gnathorhiza* in the skull-roof pattern (unpaired median B-, C-, E- and F-bones) and in details of the tooth plates (the fourth tooth ridge originates lateral to the apex). The genus *Palaeophichthys* ranges from Middle Pennsylvanian to Early Permian in east-central North America.

INTRODUCTION

In an unlikely place—a volume on the Devonian fishes of Iowa—Eastman (1908) erected the monotypic genus *Palaeophichthys* (*P. parvulus*) based on a single specimen from the Middle Pennsylvanian of the Mazon Creek area, Grundy County, Illinois. His holotype, a tiny fish on counterpart halves of a typical nodule from Mazon Creek, had been part of the S. S. Strong collection, Accession No. [222]3 of the Peabody Museum of Natural History. Donated by Yale University to the Museum of Comparative Zoology at Harvard College, it was catalogued as MCZ 5090a+b. Working from the unprepared specimen, on which much of the detail was obscured by an infilling of white kaolin, Eastman provided only a superficial description and a sketchy line drawing in which the eye and gaping mouth were wholly imaginary. The magnification of his figure was mis-stated as “ $\times 2-1$ ” instead of the actual $\times 3$ (Schevill, 1932). In default of morphological detail, Eastman attempted to classify his new genus, *Palaeophichthys*, mainly on the basis of a median fin, in which the dorsal is confluent with the caudal and anal. He mentioned a similar confluent unpaired fin in the dipnoans *Phanero-pleuron* and *Uronemus*, but found other features that suggested affinities with coelacanth. “On the whole,” he concluded, “the most plausible interpretation of *Palaeophichthys* seems to be to regard it as an aberrant and extremely degenerate offshot of fringe-finned ganoids adapted to a mud-groveling mode of existence” (Eastman, 1908:254).

In a subsequent publication, Eastman (1917:272–273) added to the hypodigm of *Palaeophichthys parvulus* a second and topotypic specimen, USNM 4433 (*sic*, mis-cited as “4453”) in the R. D. Lacoe collection at the National Museum of Natural History, Smithsonian Institution. From its water-worn condition this specimen, a half-nodule, appears to have been recovered from the bed of Mazon Creek itself. Aside from observations on the gross form and squamation of the fish, his second paper added no further information on its morphology or system-

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Submitted 23 November 1992.

atic position. "This peculiar crossopterygian genus," Eastman observed, "has been previously referred to the Coelacanthidae, but is distinguished from all other members of the family by its elongate, anguilliform body and continuous median fins. In the latter respect an agreement is to be noted with the specialized and problematical genus *Tarrasius*, from the Lower Carboniferous of Scotland, and also with *Conchopoma gadiforme* Kner, from the Lower Permian of Rhenish Prussia. Possibly both *Tarrasius* and *Conchopoma* should be regarded as aberrant coelacanth." The second specimen was illustrated by a retouched and slightly reduced photograph that reveals little morphological detail.

Lacking a proper description, later authors followed Eastman in assigning *Palaeophichthys* to either the Actinistia (coelacanth), to primitive actinopterygians (*Tarrasius*), or to the Dipnoi (*Conchopoma*). Jordan (1923) and Hay (1929) placed the Tarrasiidae with *Palaeophichthys* within the Actinistia; Zittel (1923, 1932) cited *Palaeophichthys* as probably within the Coelacanthidae. After Moy-Thomas (1934) demonstrated that *Tarrasius* is, in fact, a primitive actinopterygian, *Palaeophichthys* was regarded as an actinopterygian by Berg (1936), Romer (1945), Moy-Thomas and Miles (1971), and Bardack (1979). Jessen (1973) did not assign the genus to any group despite comparison with *Tarrasius* and other forms with a continuous fin fold, and Lehman had a similar approach (1966: "not a crossopterygian"). As the third group used for comparison by Eastman (1908, 1917), the dipnoans were suggested as the proper place for *Palaeophichthys* by Vorobyeva and Obruchev (1964: within Ctenodontidae together with *Ctenodus*, *Tranodis*, *Sagenodus*, *Megapleuron*, *Proceratodus*, and *Nielsenia*), Romer (1966: Dipnoi incertae sedis), Baird (personal communication in Bardack [1979:511]: "a senior synonym of the dipnoan *Conchopoma edesi* . . ."; and in Schultze and Bardack [1987:1]: ". . . a dipnoan, probably a new genus") and Carroll (1987:Dipnoi incertae sedis).

For most of the past half century, the type specimen has been inaccessible to researchers, having been borrowed around 1938 by T. Stanley Westoll of the University of Newcastle-upon-Tyne, England. Professor Westoll retired without publishing his conclusions on the affinities of *Palaeophichthys*, and in 1985 the specimen was returned. With the newly repatriated specimen in hand, the present restudy was undertaken to establish the true affinities of the fish.

The type and hypotype specimens have been prepared by removing the encrusting kaolin from the nodules with porcupine quills, insect pins, and small bristle brushes. Red latex casts (Baird, 1955) were then made from the natural molds.

SYSTEMATIC PALEONTOLOGY

Subclass Dipnoi Müller, 1845

Family Gnathorhizidae Miles, 1977

Genus *Palaeophichthys* Eastman, 1908

Synonym: *Monongahela* Lund, 1970

For synonymy list see Schultze (1992:200–201)

Diagnosis. — Gnathorhizid dipnoan with four unpaired median skull roof bones (B, C, E, and F). Pterygoid tooth plate with four ridges, the most posterior (fourth) ridge originating posterolaterally to the apex, whereas the other three diverge

anterolaterally. Prearticular tooth plate with three ridges. Elongated body (depth = 9.5–12.5% of total length; head length = 14–15% of total length).

Range.—Early Westphalian D to Wolfcampian, Permo-Carboniferous.

Type species.—*P. parvulus* Eastman, 1908.

Palaeophichthys parvulus Eastman, 1908

Palaeophichthys parvulus, Eastman, 1908:253, fig. 37.

P. parvulus, Eastman, 1917:272, Pl. 10, fig. 2.

P. parvulus, Schevill, 1932:85.

P. parvulus, Vorobyeva and Obruchev, 1964:314.

P. parvulus, Jessen, 1973:177.

P. parvulus, Schultze, 1992:201.

Diagnosis.—Angle between first and second ridge of pterygoid tooth plate 40°, and between second and third ridge 28°.

Stratigraphic Position and Locality.—Francis Creek Shale, Carbondale Formation, Westphalian D, Middle Pennsylvanian; Mazon Creek area, Grundy County, Illinois, U.S.A.

Holotype.—MCZ 5090 a,b, complete specimen.

Holotype.—USNM 4433, poorly preserved complete specimen.

DESCRIPTION

A small, typical Mazon Creek concretion contains the holotype in part and counterpart; only one part of the concretion of the hypotype is preserved. As common for Mazon Creek, only the molds of the bones are preserved. The description is therefore based on latex casts prepared by Donald Baird, and the bones are described as if they are preserved three-dimensionally. The holotype is better preserved than the hypotype; thus the description refers mainly to the part and counterpart of the holotype.

The specimens are elongate but not eel-like as described by Eastman (1908). The holotype (Fig. 1) is 3.6 cm long with a depth of 0.45 cm, the hypotype is 5.2 and 0.7 cm, respectively. The head is 5.5 mm long (7.4 mm in hypotype), less than 1/6 of the total length. The part (MCZ 5090a) shows the right side of the specimen (MCZ 5090 a, Fig. 2), with the skull roof seen in oblique dorsal view; a smooth ostracod lies at the approximate place of the stomach. The counterpart (MCZ 5090 b, Fig. 3) shows bones of the left side and internal views of bones of the right side of the skull roof in oblique ventral view, and bones of the palate, gill arches, and shoulder girdle. Despite the small size, the skull roof, palate, and ceratohyal are fully ossified, and the complete body covered by scales.

Skull Roof (Fig. 2).—The skull roof displays three median bones, broad B- and C-bones, and a narrower E-bone. Only the inner side of the lateral portion of these bones can be seen in the hypotype. The posterior part of bone B, with its occipital commissure, is missing. The counterpart (Fig. 3) shows the impression of two small bones anterior to bone E, a median F-bone and the right lateral Q-bone with large evaginations for the pores of the supraorbital canal. The three median bones are displaced laterally over their neighboring bones toward the wide groove of the lateral line (Fig. 2). Only part of the inside of the left I and J bones, and part of the right J-bone in the corner between bones B and C are exposed. The anterior part of bone Z carries the broad lateral line canal, whereas the branching-off of the occipital commissure is only weakly preserved. In front of



Fig. 1.—*Palaeophichthys parvulus* Eastman, 1908. Latex cast of holotype MCZ 5090a dusted with NH_4Cl .

bone Z lies a small bone Y, followed anteriorly by a longer, only partly preserved X-bone. The pattern of the skull roof cannot be restored from the two specimens.

Cheek.—Because only a few bones are preserved behind the orbit, the cheek pattern cannot be established.

Lower jaw.—The right “angular” is completely preserved on the right side (Fig. 2), whereas only the posterior part of the left “angular” is preserved on the counterpart (Fig. 3). The position of the mandibular canal is marked as a deep

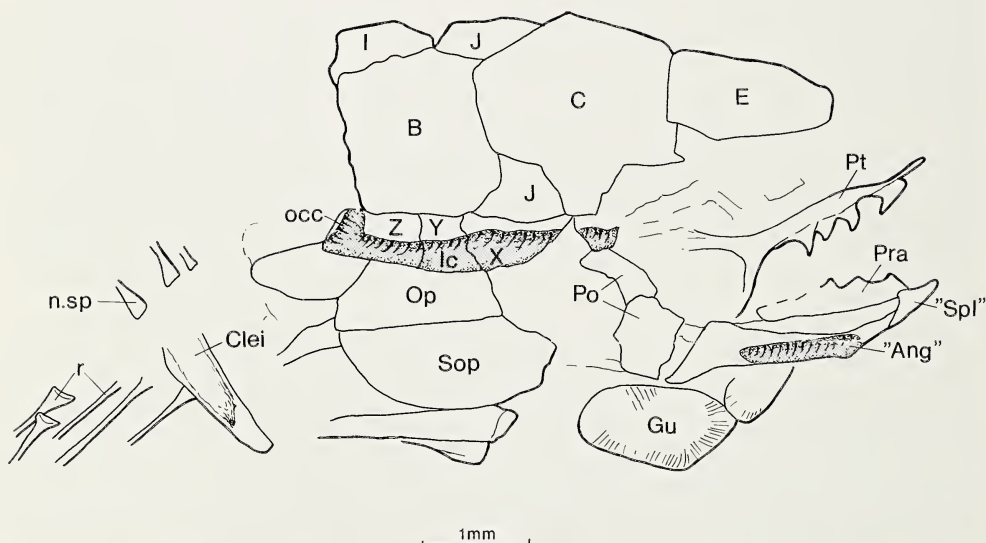


Fig. 2.—*Palaeophichthys parvulus* Eastman, 1908. Head of holotype MCZ 5090a. Abbreviations: “Ang,” angular; B, C, E, I, J, X, Y, Z, skull-roof bones; Clei, cleithrum; Gu, gular; lc, main lateral canal; n.sp, neural spine; occ, occipital commissure; Op, operculum; Po, postorbital bone fragments; Pra, prearticular; Pt, pterygoid; r, rib; Sop, suboperculum, “Spl,” splenial.

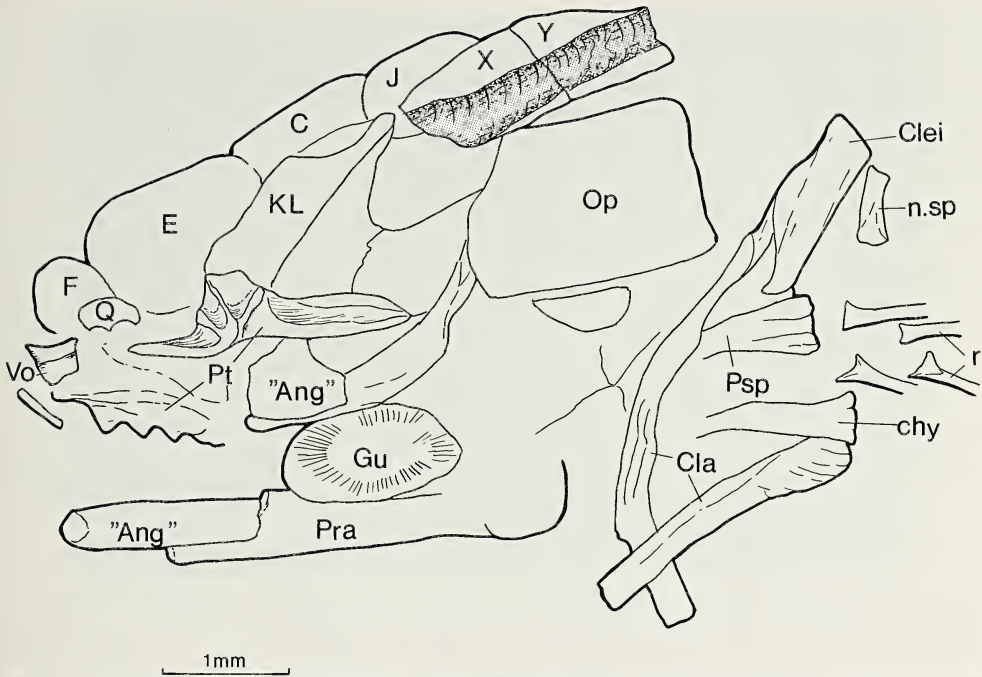


Fig. 3.—*Palaeophichthys parvulus* Eastman, 1908. Palate and shoulder girdle regions of holotype MCZ 5090b. Abbreviations: "Ang," angular; C, E, F, J, KL, Q, X, Y, skull roof bones from the inside; chy, ceratohyal; Cla, clavicle; Clei, cleithrum; Gu, gular; n.sp, neural spine; Op, operculum; Pra, prearticular; Pt, pterygoid; Psp, parasphenoid; Vo, vomer.

groove on the "angular." Anterior to the "angular" the "splenial" reaches anterolaterally to the prearticular. The labial side of the right prearticular is exposed partially on the part and the lingual side on the counterpart. The prearticular tooth plate is only seen in lateral view; it bears three ridges.

Palate.—Opposed to the tooth plate of the lower jaw, the tooth plate of the right pterygoid shows indication of four ridges. These ridges are clearly visible on the left pterygoid (Fig. 3, 4). A long anterior ridge is combined with three short ridges that are directed anterolaterally and posterolaterally. The first three ridges diverge from the apex of the tooth plate, whereas the most posterior ridge originates laterally to and lower than the apex. The ridges show indications of cusps. The angles between the first and second, second and third, and third and fourth ridges are 40°, 28°, and 55°, respectively. The posterior flange of the pterygoid has a steep medial side and a narrow width. The vomerine tooth is located on a pointed, anteriorly directed base in front of the anterior ridge of the pterygoid tooth plate. No cusps are visible at the margin of the vomerine tooth plate. Only the most posterior end of the parasphenoid is visible between the bones of the shoulder girdle anterior to the ribs.

Opercular and Gular Region.—The counterpart (Fig. 3) shows a large operculum, which is anteroposteriorly longer than dorsoventrally deep (4:3). The suboperculum, preserved on the part below the operculum, is as long as the operculum, but much lower in depth (5:2). The suboperculum is the best preserved bone in the hypotype and has the same shape and size relations as in the holotype.

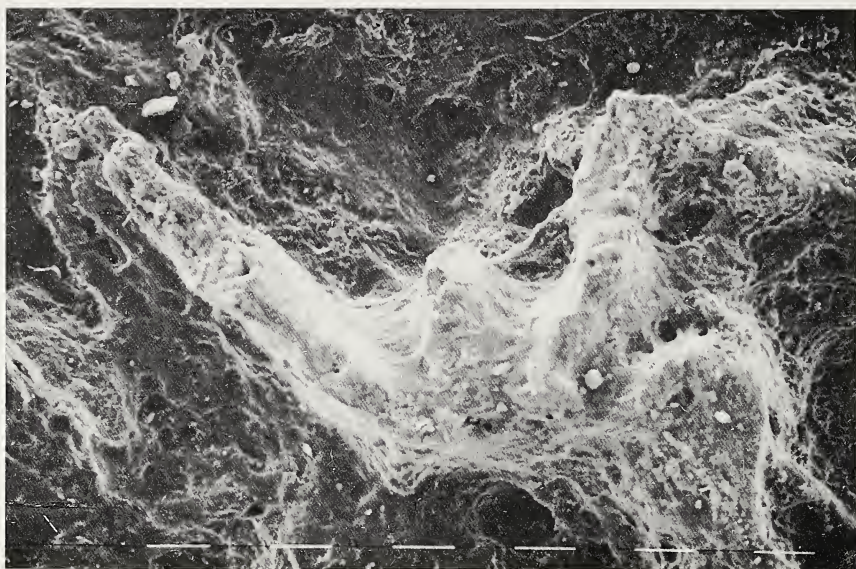


Fig. 4.—*Palaeophichthys parvulus* Eastman, 1908. SEM of Latex cast of holotype MCZ 5090b, left pterygoid tooth plate; $\times 72$ (each white line corresponds to 100 μm).

Part and counterpart show indications of a lateral gular adjacent to clearly preserved principal gulars. The principal gular plate shows striations radiating toward the margin. The ceratohyal is completely visible in the hypotype, but only the posterior part is in the holotype (Fig. 3). It is an elongated bone with narrow middle portion and expanded anterior and posterior ends.

Postcranial Skeleton.—The shoulder girdle of the holotype (Fig. 3) and hypotype consists of a relative short, broad, massive cleithrum and a long, narrow clavicle. The clavicle widens dorsally, where it overlaps the ventral part of the cleithrum. The body of the part and counterpart of holotype and hypotype shows a complete covering of scales. The scales (Fig. 5) are round and elongated, with parallel ridges on the anterior covered field and converging ridges on the posterior exposed field. They show the division in fields typical for post-Devonian dipnoans. Ribs extend posteriorly from the shoulder girdle 40–50% of the body length and indicate the extent of the abdominal cavity. The weakly ossified series of spines extends posteriorly nearly as far back as the ribs.

Paired fins or their traces are not preserved in either specimen. A continuous fin fold surrounds the posterior part of the body. Dorsally it occupies 60% of body length and ventrally 42%. There are no supporting elements visible for the fin fold. The lepidotrichia are not articulated and also seem not to bifurcate.

AGE

Lund (1970, 1973) described age pattern in tooth plates of *Palaeophichthys* (*Monongahela*) *stenodonta* and *dunkardensis*. In both species the number of cusps increases with size increase of tooth plates; the cusps are worn in larger tooth plates. The fourth ridge of the pterygoid plate appears late in subadult stage (Lund, 1970:253). This ridge is developed in *P. parvulus*, which indicates that we are dealing at least with subadult, if not adult, specimens, despite their small size.

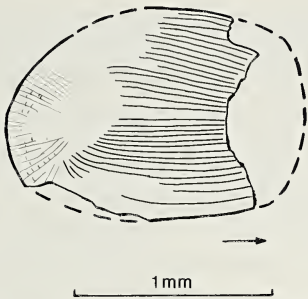


Fig. 5.—*Palaeophichthys parvulus* Eastman, 1908. Scale of holotype MCZ 5090 from the middle of the body above the beginning of the anal fin.

Further indications of subadult or adult stage are the full ossification of skull roof, palate, and ceratohyal; the complete covering of the body by scales; and the lack of cusps on the vomerine tooth.

COMPARISON

Palaeophichthys parvulus is a tooth-plated dipnoan (after the terminology of Campbell and Barwick, 1983), and has no relationship to the denticulated dipnoan *Conchopoma*. The tooth plates of *Palaeophichthys* resemble those of gnathorhizids, and the tooth plate of the pterygoid agrees with the diagnosis of the gnathorhizid genus *Monongahela* (Lund, 1970) in that the most posterior fourth ridge originates laterally to the apex of the tooth plate. On the basis of this evidence, *Monongahela* is, therefore, considered a junior synonym of *Palaeophichthys*. The genus *Monongahela* was described at a time when the true nature and affinities of *Palaeophichthys* were entirely unknown. *Palaeophichthys parvulus* is distinct from the two species *P. stenodonta* and *P. dunkardensis* described by Lund (1970, 1973): it has a different angle between the ridges of the tooth plates, different shape of cusps on the ridges (Table 1), and different position of the fourth ridge. Differences in cusp shape also occur on the vomerine tooth plate. The most posterior fourth ridge of *P. parvulus* originates closer to the apex than in the other two species.

The skull roof pattern of *Palaeophichthys* is unique within Paleozoic dipnoans in having three, possibly four, median unpaired bones (B, C, E, and F): in *Sagenodus* and *Conchopoma* bones B and C are unpaired, but bone E is paired; in *Megapleuron* and *Gnathorhiza* bones B and E are unpaired, but bone C is paired; whereas *Ctenodus* and *Tranodis* have paired C- and E-bones. The composition

Table 1.—Comparison of the pterygoid tooth plates of the three species of *Palaeophichthys*. * Data from Lund (1970, 1973).

	Angle between 1. a. 2. ridge (range)	Angle between 2. a. 3. ridge (range)	Shape of cusps on ridges
<i>P. dunkardensis</i> *	14.37 (7–28)	15.49 (9–32)	rounded
<i>P. stenodonta</i> *	41.65 (12–60)	48.35	laterally flattened
<i>P. parvulus</i>	40	28	distinct

of the lateral-line bones differs from *Gnathorhiza*: the occurrence of Z-, Y-, X- and elongate KL-bones is more primitive than the reduction to fewer larger bones in *Gnathorhiza* (Berman, 1976). The length/depth relations of operculum and suboperculum also are different in the two genera: the operculum is longer than deep in *Palaeophichthys*, whereas it is deeper than long in *Gnathorhiza*. On the other hand, *Palaeophichthys* possesses a broad cleithrum and a very elongated clavicle, as does *Gnathorhiza* (Berman, 1976).

In summary, *Palaeophichthys* (= *Monongahela*) is distinct in its skull roof pattern from other Paleozoic dipnoans, but the tooth plates indicate close relationship to *Gnathorhiza*.

CONCLUSIONS

Palaeophichthys becomes the fourth identifiable dipnoan genus from the Middle Pennsylvanian of the Mazon Creek area, joining *Conchopoma* (Denison, 1969; Schultze, 1975), *Ctenodus* (Baird, 1978), and *Megapleuron* (Schultze, 1977). However, it is now well understood that two ecologically distinct assemblages constitute the Mazon Creek fauna (Johnson and Richardson, 1966). On present evidence, *Palaeophichthys* is restricted to the Braidwood fauna, a nonmarine association that is found in the more northerly area of deposition, including the beds along Mazon Creek in Grundy County. *Conchopoma* and *Megapleuron*, on the other hand, are found only in the marginal-marine Essex fauna, which is best known from Pit Eleven in Will and Kankakee counties, whereas *Ctenodus* is recorded from both assemblages. Although *Megapleuron* is otherwise known only by two specimens from another Pennsylvanian locality in North America (Linton, Ohio: specimen 063.107-2 in David S. Hamilla's private collection) and from the Lower Permian of France, *Conchopoma* and *Palaeophichthys* occur commonly in other Paleozoic localities of North America. *Conchopoma* is known from the Middle Pennsylvanian of Linton (Schultze, 1977; Hook and Baird, 1986) and Five Points (Hook and Baird, in press), Ohio, and from the Upper Pennsylvanian of Vermilion County, Illinois (Schultze, 1977). *Palaeophichthys* was described as *Monongahela* from the Upper Pennsylvanian of Allegheny County and the Lower Permian of Washington County, Pennsylvania (Lund, 1970, 1973). It is surprising that only two specimens of *Palaeophichthys* have been found in the thousands of concretions from the Mazon Creek area.

ACKNOWLEDGMENTS

The author is grateful to the chain of persons who delivered the holotype of *Palaeophichthys parvulus* into his hands: Alick D. Walker, Robert W. Hook, Charles R. Schaff, Mary Ann Turner, S. Christopher Bennett, and Donald Baird. Donald Baird contributed to the introduction and prepared the peels. Robert W. Hook, Richard Lund, and Jiri Zidek have helpfully criticized the manuscript. John Chorn kindly photographed the holotype. J. Elder and J. Wigglesworth, Word Processing Center, Division of Biological Sciences, The University of Kansas, kindly typed different versions of the manuscript. The author thanks the National Science Foundation for partial support of the project through grant BSR-8806856.

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EXPLOITATION OF MAMMALS AT THE EARLY BRONZE AGE SITE OF WEST ROW FEN (MILDENHALL 165), SUFFOLK, ENGLAND

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ABSTRACT

The large assemblage of faunal material from the Early Bronze Age site of West Row Fen (Mildenhall 165) in Suffolk, England, provides important data on the economy and subsistence during a poorly known time period in Great Britain. Dominated by gracile, short-horned cattle and small, Soay-sized two-horned sheep, this primarily domestic fauna demonstrates that by this period there was minimal dependence on hunting in comparison to stock rearing. Other common domesticates in the assemblage are goats, pigs, and dogs. Wild species that were hunted include hare, red deer, roe deer, and aurochs, the latter represented by only one extremely large humerus. It is unclear whether horses at West Row Fen were domestic or wild. Preserved carnivores include the wild cat, red fox, and domestic dog. The presence of the western hedgehog, the western mole, and the water vole suggests a wet woodland habitat typical of the fens during this period.

Aging of the domestic livestock by epiphyseal fusion and dental eruption and wear show differential treatment of cattle, sheep and goats, and pigs. Cattle were probably used more for draft than for their dairy products, whereas sheep or goats were being milked. Most pigs were slaughtered in their first year of life to control population growth, although some were allowed to reach reproductive maturity and were killed as needed.

Major taphonomic processes included carnivore gnawing, sedimentary abrasion probably caused by trampling, moderately light root-etching, and, more rarely, erosion, weathering, and rodent gnawing. Butchering patterns, previously poorly known from the Bronze Age of Britain, suggest that cow horns were heavily utilized, metal axes may have been used on cattle carcasses, and dogs were eaten. Pathologies are those frequently associated with domestic animals, such as malocclusions, tooth anomalies, and bone modification caused by heavy draft. A total of 120 bone and antler artifacts were identified, including awls, a pin, a scoop, a spatula, tubular beads, a dagger, pressure-flakers, a handle, socketed mace-heads, and a wedge.

INTRODUCTION

West Row Fen contains a remarkably well-preserved Early Bronze Age village that reveals much about the lives of its inhabitants. Located in Suffolk County just west of the modern town of Mildenhall (Fig. 1), the site had been protected for centuries by an overlying cap of Iron Age peat. The fen was drained in 1759, and erosion subsequently removed much of the peat (Martin and Murphy, 1988: 353), exposing the richness of Neolithic and Bronze Age settlements in the fenlands around West Row. Although plowing has damaged and destroyed most of these prehistoric deposits, one site, Mildenhall 165, remained relatively undisturbed.

Major excavations of the site were first undertaken in 1982 and continued through 1986. The archaeological work was conducted by the Suffolk Archaeological Unit and English Heritage, under the supervision of Dr. Edward Martin. Approximately 4200 m² were excavated, yielding over 31,000 pieces of animal bone. All lithic and bone artifacts were recorded three-dimensionally using a reference datum, and unworked faunal material was recorded by feature, layer within a feature, or 1-m² unit.

Submitted 9 December 1992.

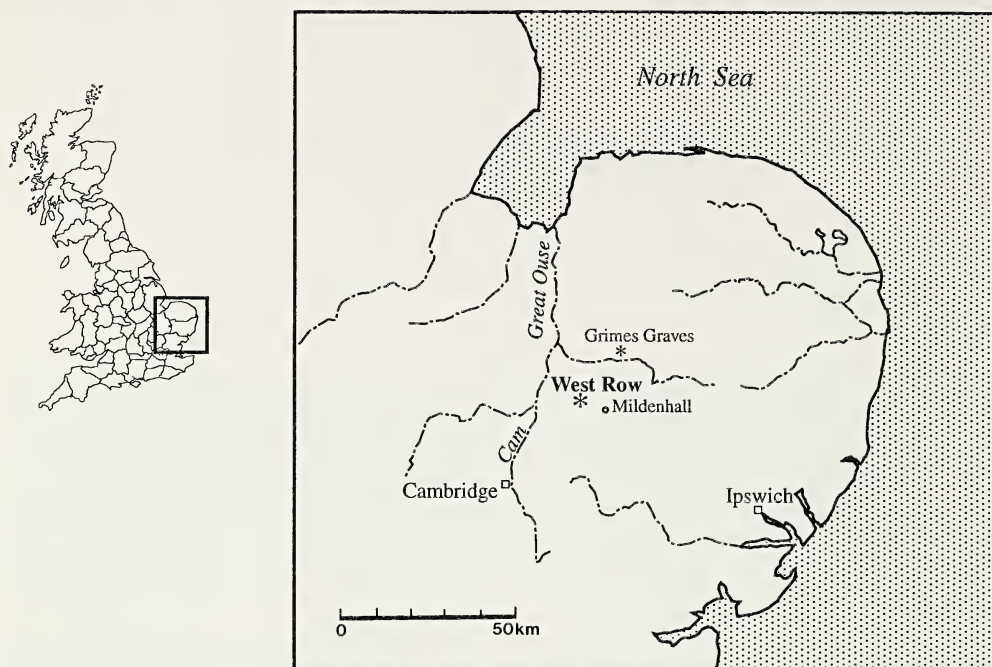


Fig. 1.—Map of East Anglia showing the location of the site of West Row Fen.

The site lies primarily on a penannular sand ridge about 2.3 m above an adjacent hollow. While some plow damage was noted on top of the sand ridge, most of the deposits were intact at lower elevations. Some of the deepest features lie below the water table and therefore contain well-preserved organic matter.

A small lithic scatter of Mesolithic age and a few Neolithic pits and lithic scatters were found, but the village dates predominantly from the latter part of the Early Bronze Age. Radiocarbon dates for the Early Bronze Age component place it at ca. 2290–1780 B.C., calibrated.

The environment in the vicinity of the site can be inferred from the preserved wood, macrobotanical remains, pollen, terrestrial mollusks, and small vertebrates. The rich woodlands surrounding the site included oaks on the higher ground and alders on lower elevations. After the village land was cleared, wet tussock conditions persisted. Scrub and wet woodland plants such as elder, hazel, holly, sloe, and willow were also present around the periphery. Cultivated plants consisted primarily of emmer wheat, accompanied by spelt wheat, hulled barley, and flax (Martin and Murphy, 1988:356).

The remains of mollusks, fish, amphibians, reptiles, and birds are still undergoing investigation by other researchers, but do not contradict environmental indications from plant remains. The microfauna from flotation and fine screening, containing numerous rodents and insectivores, is also being analyzed separately and is excluded from this study.

Portions of three round houses fabricated from light timber were found on the ridge (Fig. 2). The most complete was about 5 m in diameter and had a porch on the south-east side (Martin and Murphy, 1988:355). A midden area filled one of the lower parts of the site.

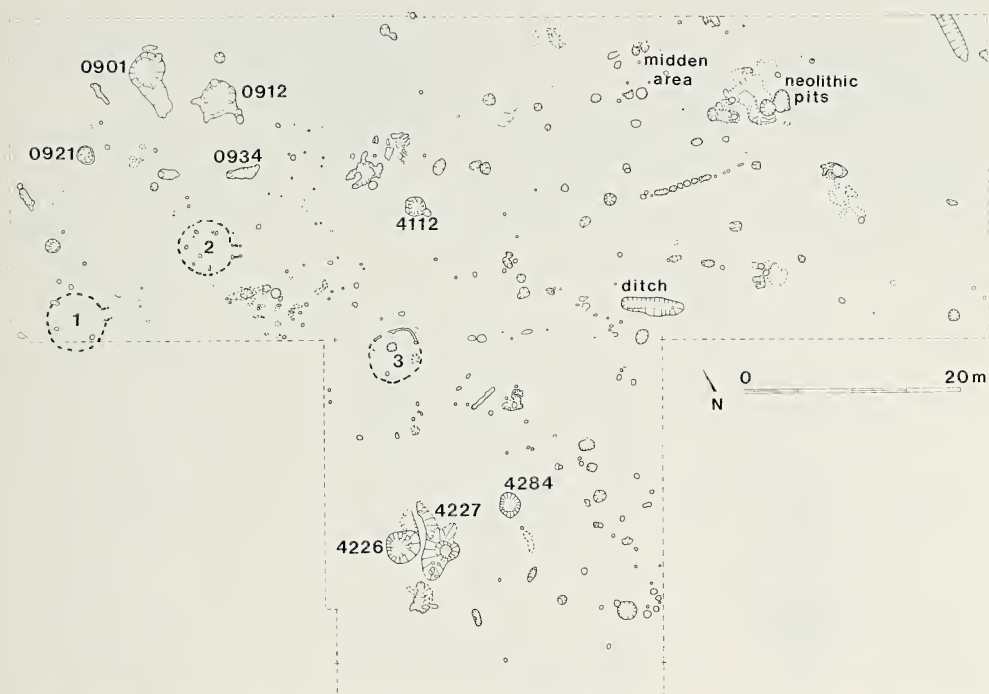


Fig. 2.—Plan of excavated area showing locations of features and houses. Key to features: 1, house; 2, house; 3, house; 0901, water pit; 0912, water pit; 0921, flax retting pit; 0934, charcoal clamp; 4112, water pit filled with ash and charcoal; 4226, large water pit; 4227, large feature containing water pit; 4284, antler soaking pit.

The most informative features were the numerous pits distributed over the site (Fig. 2). The dry pits along the ridge contained charcoal, animal bones, potsherds, flint, and other domestic debris. The wet pits (0901, 0912, 4112, 4226, 4227, and 4284) in low-lying areas of the site served several functions. Some were lined with alder logs to support the sidewalls and allow easy access, and probably functioned as shallow wells. Pit 0921 contained seeds and fragments of flax (*Linum usitatissimum*) and appears to be the oldest known retting pit in Britain (Martin and Murphy, 1988:355). Pit 4284 (diameter, 2 m; depth, 1.05 m), contained a split red deer antler (length, 42 cm) that was apparently placed in water to soak prior to undergoing further manufacturing.

The stone implements recovered include scrapers, knives, saws, borers, arrow-heads, mace-heads, hammerstones, querns, and rubbing stones (Martin and Murphy, 1988:355). Seven small jet toggles, ranging from 1.3 to 2.3 cm in length, may have served as earrings or buttons. Pottery was mostly Grimston-type plain ware.

The large assemblage of mammalian fauna from West Row Fen, Mildenhall 165, documents a heavy dependence on domestic species in the Early Bronze Age with a secondary reliance on wild animals to supplement the diet. At present, few large collections from the British Bronze Age have been studied. The material from the Middle Bronze Age deposit at Grimes Graves, in Norfolk (Legge, 1981, 1992), and from the Late Bronze Age layers at Runnymede in Surrey (Done, 1991, Serjeantson, 1991) are the most notable exceptions.

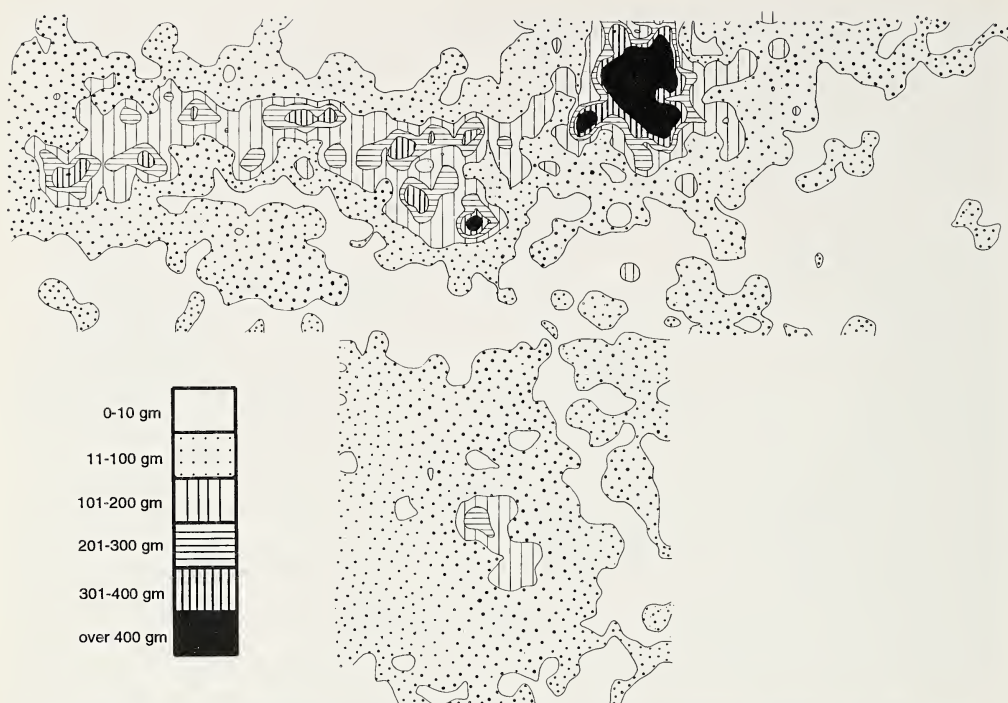


Fig. 3.—Distribution of animal bone fragments throughout the excavated area of the site.

SPATIAL DISTRIBUTION OF MAMMALIAN FAUNA IN SITE

The unmodified faunal material was distributed unevenly across the site (Fig. 3; Table 1). The densest concentrations were just west of the midden area, but the midden itself and the area around the flax-retting pit, water pits, and a charcoal clamp in the western part of the site also contained considerable amounts of animal bone. Another concentration was found during the 1985 excavations in the southern part of the site around the antler soaking pit. Three of the pits (0901, 0912, and 4226) contain large numbers of bones, suggesting that the pits were filled in with food refuse when their original function ended. The species repre-

Table 1.—Number of identifiable bone fragments in features.

Feature	<i>Canis</i>	<i>Sus</i>	<i>Capreolus</i>	<i>Cervus</i>	<i>Ovis/Capra</i>	<i>Bos</i>
House 1			1	3	1	1
House 2		1	1		4	4
House 3		2			3	1
Pit 0901		8	2		25	40
Pit 0912		6		1	29	70
Pit 0934						9
Pit 4112					2	1
Pit 4226	8	2		4	39	51
Pit 4227	1				2	5
Pit 4284	2			1	3	4
Neolithic pits						3
Ditch		5			2	5

Table 2.—Frequencies of mammalian taxa from West Row Fen.

Taxon	NISP	% of NISP ^a	MNI	% of combined MNI (175)	Individual usable meat (kg) ^b	Combined usable meat (kg) ^c
Class Mammalia	23,189	n.a.	n.a.			
<i>Erinaceus europaeus</i>	3	<1	2	1		
<i>Talpa europaea</i>	1	<1	1	1		
<i>Lepus</i> , cf. <i>L. capensis</i>	19	<1	3	2	2.25	6.75
Order Rodentia	10	<1	n.a.	—		
<i>?Arvicola terrestris</i>	14	<1	2	1		
<i>Felis sylvestris</i>	4	<1	1	1		
<i>Vulpes vulpes</i>	9	<1	1	1		
<i>Canis familiaris</i>	81	1	5	3	5	25
<i>Cervus</i> , <i>Bos</i> , or <i>Equus</i>	979	12	n.a.	—		
Order Artiodactyla	29	<1	n.a.	—		
<i>Sus scrofa</i>	757	9	21	12	15	315
Suborder Ruminantia	1198	14	n.a.	—		
Family Cervidae	4	<1	n.a.	—		
<i>Capreolus capreolus</i>	69	1	6	3	10.5	63
<i>Cervus elaphus</i>	139	2	5	3	95	475
Family Bovidae	25	<1	n.a.	—		
<i>Capra hirc</i> a	6	<1	2	1		
<i>Ovis aries</i>	52	1	9	5		
<i>Ovis</i> / <i>Capra</i>	1617	20	60 ^d	34	12.5	750
<i>Bos primigenius</i>	1	<1	1	1	450	450
<i>Bos taurus</i>	3230	39	55	31	350	19,250
<i>Equus caballus</i>	15	<1	1	1	300	300
Totals	31,451		175			

^a *n* = 8262 fragments (excludes those only identifiable to Class Mammalia).
^b Usable meat weight for an average adult individual (based on Milisauskas, 1978).
^c Usable meat for the species is calculated by multiplying the usable meat weight per individual by the MNI for that species.
^d MNI recalculated to combine *Ovis*/*Capra* (MNI = 59), *Ovis aries*, and *Capra hirc*a.

sented in the pits were domesticates, red deer, and roe deer, all of which appear to have been consumed by the inhabitants. The areas in and around the houses were kept remarkably clean of animal remains. One possibly significant intraspecific concentration of bones was a cluster of eight dog bones in water pit 4226, which probably represents food refuse. Animal burials and ceremonial treatment of animal remains were not observed. Bones of wild species, such as hare, red deer, and roe deer, were scattered and distributed in the same pattern as the domestic species.

METHODOLOGY

In order to determine relative frequencies of mammalian species at West Row Fen, both the NISP (number of identified specimens) and the MNI (minimum number of individuals) were calculated (Grayson, 1979). The MNI was calculated using a zone technique, which records the portions of each bone present in detail (Dobney and Rielly, 1988). Each bone is divided into zones according to diagnostic features and the ways in which bones break most frequently. To calculate MNIs the number of times a zone appears for the left and right bones is counted separately. The zone with the largest number (for either the left or the right element) yields the MNI for that bone. The MNI for a species is the count from the bone with the highest MNI. Table 2 lists the taxa identified, followed by the NISP and

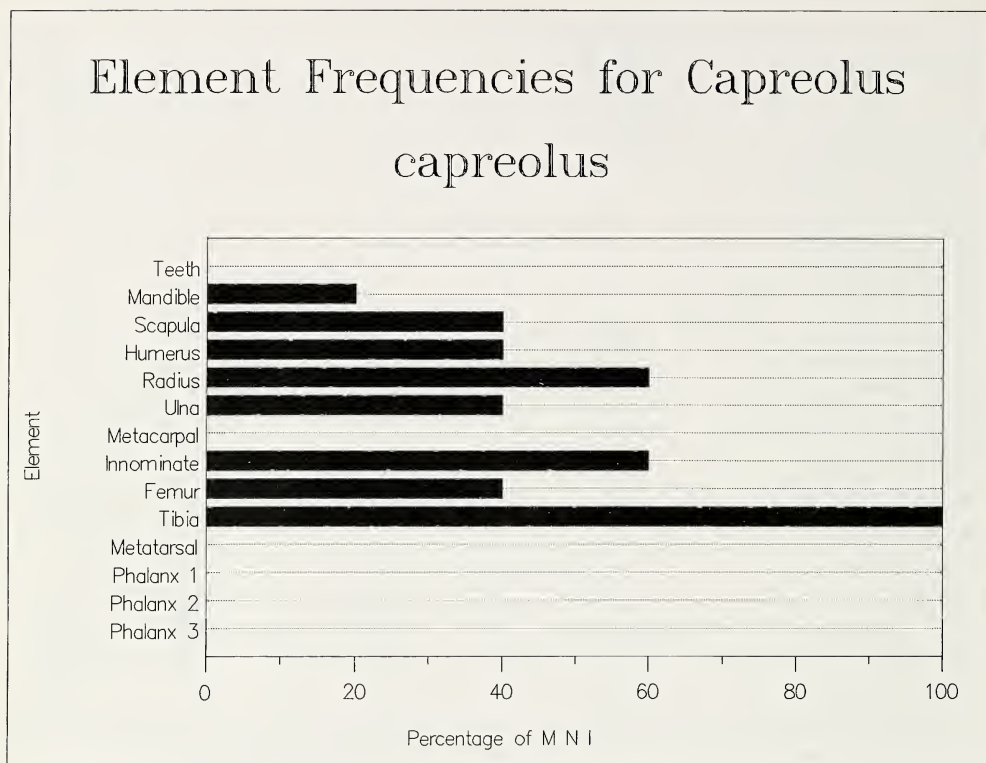


Fig. 4.—Element frequencies for *Capreolus capreolus*.

MNI for each taxon by absolute numbers and percentages of identifiable mammalian fauna (excluding those elements only identified to Class Mammalia).

Table 2 also lists the estimated weight of usable meat in each of the food-producing species. According to this measure, cattle were clearly the most important food species at West Row Fen, followed by sheep and goats, and then red deer. The single aurochs would have yielded as much meat as 36 sheep or goats. Pigs, which are third most abundant, rank fifth in meat yield. However, meat yield must be considered in a temporal context. For example, despite the enormous dietary contribution made by a single wild aurochs, it represents only one event that would provide a windfall for a few weeks or even months if the meat was smoked or dried. But aurochs and other wild game would not be as consistently available as domestic pigs. Domestic animals are “walking larders” and can provide a secure food source in periods of environmental stress when wild species cannot. Calculating the actual amount of meat consumed at West Row Fen using estimated weight of usable meat is a technique fraught with problems (Guilday, 1970) and is not attempted here.

Element frequencies (Fig. 4–8) are useful in contrasting butchering patterns and body part utilization between hunted and domestic species, especially when the hunted species are field dressed to lessen the burden of hauling home a whole carcass, and domestic species are killed near the village. This calculation pertains more to red deer than roe deer, which are easily carried back whole. There was no clear evidence of field dressing or discarding of bones of low utility in this assemblage.

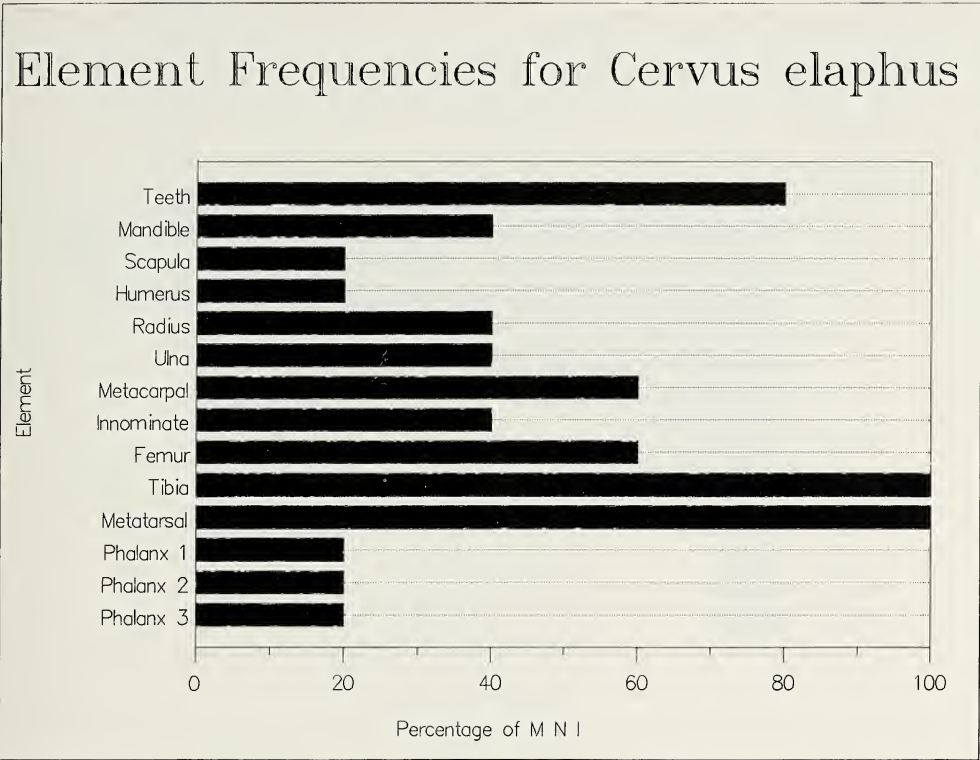


Fig. 5.—Element frequencies for *Cervus elaphus*.

Figures 4–8 imply differential preservation due to various taphonomic factors. Phalanges are poorly preserved but teeth are in abundance, implying that the low number of phalanges was caused by natural or cultural processes rather than inferior recovery techniques. Phalanges have marrow cavities and are easier to break than teeth. Dogs may have chewed on the phalanges, destroying them or leaving only undiagnostic fragments. Humans may also have reduced the phalanges beyond recognition with hammerstones while retrieving the marrow. Distal tibiae were very well-represented, probably because they are very dense and resist destruction. Flat elements constructed of thin cortical bone not bolstered with considerable amounts of cancellous tissue, like the scapula, ulna, and innominate tended to be slightly less well-preserved. These elements are susceptible to breakage during excessive pedoturbation (Olsen, 1989), such as trampling in this case.

Tooth eruption and wear stages were recorded for domestic ungulates with reference to Silver (1969), Grant (1982), Bull and Payne (1982), and Legge (1992). The absence of complete tooth rows, however, impeded reconstruction of mortality patterns for all of the species at West Row Fen. In recording the wear patterns on the teeth of *Ovis/Capra* and *Bos taurus*, Grant's (1982) technique was used, but as it requires nearly complete tooth rows, final determinations of ages were made chiefly on the basis of Silver's (1969) eruption dates and information compiled by Legge (1992). Both Bull and Payne (1982) and Silver (1969) were used to age pigs. Redding's (1981) methods for calculating percentages of animals surviving past the ages of fusion for long bones was applied to the domestic animals from West Row Fen.

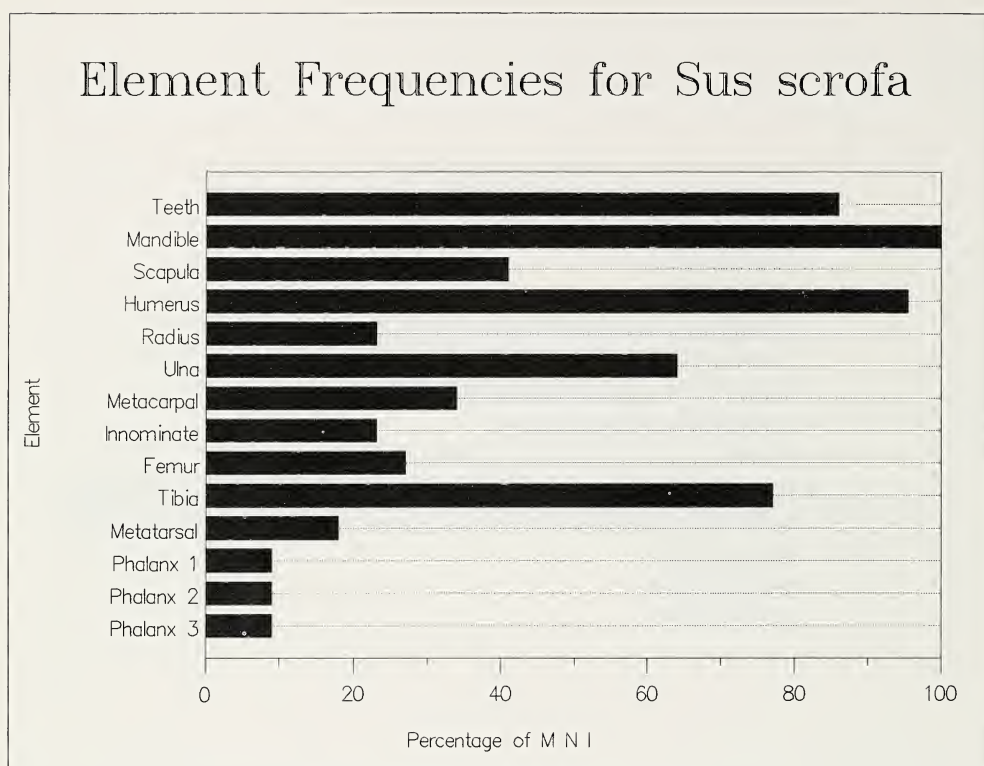


Fig. 6.—Element frequencies for *Sus scrofa*.

All fragments with butcher marks were drawn so that the orientation of each mark and the number of bones with marks in those positions could be determined. This information is summarized on illustrations of articulated skeletons for each of the three most prevalent species (Fig. 18, 20, 23). Distinctions between cut-marks, chopmarks, and scraping were noted. The best examples of each type of butcher mark were replicated by making silicone rubber molds and epoxy resin casts for examination in a scanning electron microscope.

Taphonomic traces, pathologies, and anomalies were recorded. Specific causes are difficult to attribute to pathological alterations of archaeological bone, but comparisons can be made with living individuals with known histories in order to make tentative diagnoses.

CONDITIONS OF PRESERVATION

Soil conditions at the site of West Row Fen are typical of these fenlands and are significant regarding bone preservation. The site's location in sandy deposits resting on top of chalk provides the soil with a pH that is sufficiently alkaline for bone conservation. Although less bone survived in the overlying peat layer, the peat's acidity apparently did not filter down enough to alter the sand's pH and dissolve the bone in that layer. Sand is generally not a good medium for bone preservation because the loose grains allow water to flow through too easily, but

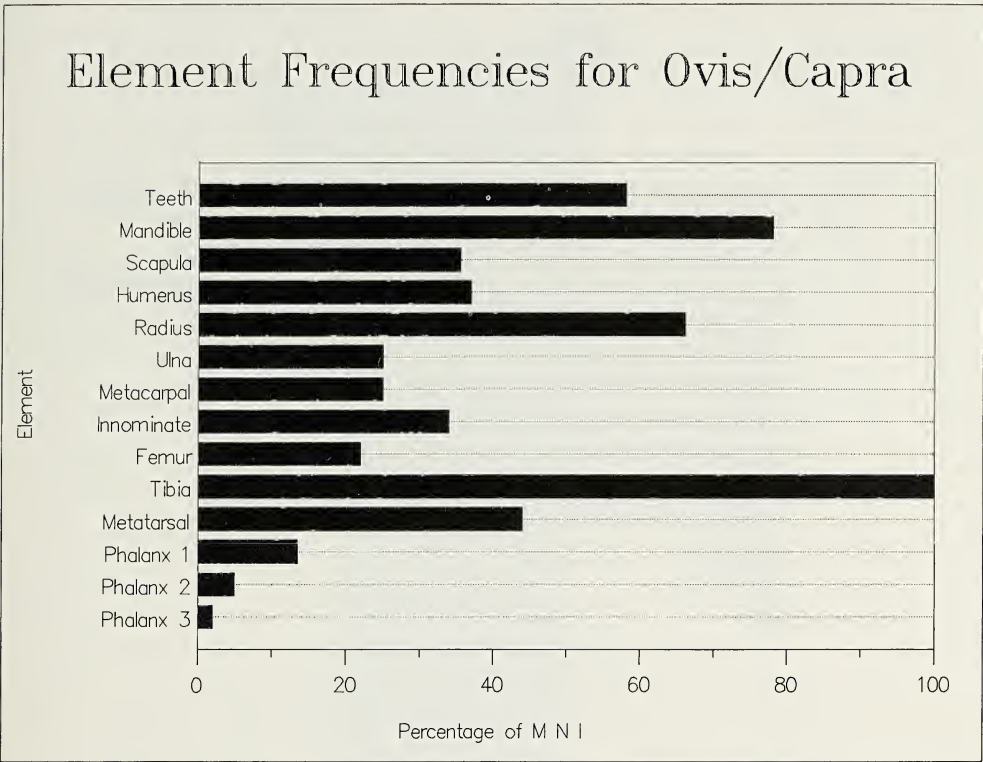


Fig. 7.—Element frequencies for *Ovis/Capra*.

in this case the chalk inhibited drainage and made the ground water alkaline enough to maintain a suitable environment for preserving bone. Mineral accretions, apparently rich in iron, were found adhering directly to some bone surfaces, but these could be removed with gentle brushing in most cases. Butcher marks as well as manufacturing and use-wear traces on bone artifacts were readily visible on the well-preserved bone surfaces.

TAPHONOMY

Despite the generally good condition of the faunal material from West Row Fen, the effects of several deleterious taphonomic agents were observed. The frequencies of taphonomic effects on identifiable bone fragments are displayed in Table 3. Of these processes, carnivore gnawing was the most destructive agent. Whole condyles of cattle bones were occasionally missing as a result of heavy gnawing (Fig. 9). Since most butcher marks occur in the epicondylar regions of long bones, many were probably destroyed as a result of carnivore activity. Carnivores probably caused impact scars and spiral fractures as often as humans, so the extent of marrow extraction by humans was difficult to assess. In this case, the most likely culprits in carnivore gnawing were the village dogs, since they are the most common carnivores in the assemblage, and foxes and wild cats were the only other carnivores identified. Because of their specialized dentition, cats rarely

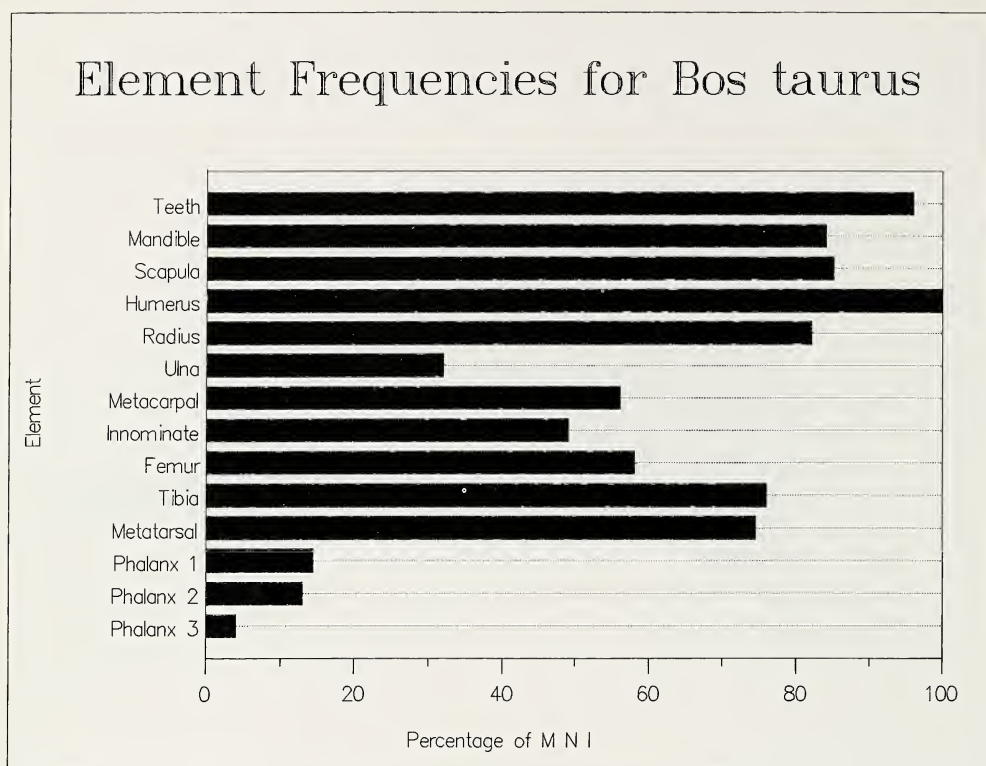


Fig. 8.—Element frequencies for *Bos taurus*.

chew on bones. Both foxes and cats are too small to have inflicted serious damage on cattle bones. Given the prevalence of severe gnawing on ungulate long bones, this taphonomic factor may explain why small toe bones, carpals, and tarsals of these species were underrepresented in the faunal assemblage (Fig. 4–8). It probably also contributed to the paucity of remains of smaller taxa such as birds, insectivores, rodents, and hares. Four small bone splinters that have a sheen extending over their broken edges and medullary surfaces appear to have been acid-etched. The best explanation is that these pieces passed through the digestive system of a carnivore (Payne and Munson, 1985; Horwitz, 1990), most likely the domestic dog.

Sedimentary abrasion was the second most destructive taphonomic process. Abrasion striations caused by the great amount of sand in the soil were often observed on bone surfaces. The cause of this abrasion is some form of pedoturbation which, given the environmental and geologic settings, most likely involved trampling by ungulates and people (Olsen and Shipman, 1988). Much of the postdepositional breakage of bones may also have been caused by trampling. Many of the cow scapulae are heavily abraded and exhibit a recurrent breakage pattern in which a V-shaped notch is broken out of the center of the blade. The mouth of the V is at the vertebral border. This breakage pattern might be expected if a hooved animal stepped on a scapular blade that was lying flat on the ground. The missing area on these scapulae represents the thinnest, weakest part of the



Fig. 9.—Carnivore gnawing on the ends of a cow radius.

blade. The scapular spine is also rarely preserved. Abrasion usually appears as sets of fine parallel striations that sweep over the bone surface rather than gouging deeply into it (Olsen and Shipman, 1988). Abrasion can vary from a polish to coarse striae as great as 1 mm in width. Although it is normally easy to distinguish between sedimentary abrasion and cutmarks, abrasion can obscure or erase evidence of butchery.

Root-etching was also distributed throughout the assemblage, but was never



Fig. 10.—Perforations in a lumbar vertebra of cow probably caused by large roots.

Table 3.—*Taphonomic modifications to identifiable bone fragments.*

Taphonomic process	NISP	% of NISP ^a
Carnivore gnawing	347	4.2
Sedimentary abrasion	333	4.0
Root etching	270	3.3
Erosion	168	2.0
Weathering	100	1.2
Rodent gnawing	6	0.1
Burning	5	0.1

^a $n = 8262$, number of identifiable bone fragments, excluding bones identified only as Class Mammalia.

dense on any given bone fragment. The small dendritic grooves, etched by the acid produced at the tips of rootlets, indicate that there had been a ground cover of vegetation shortly after the bones were deposited. This is also evident from the peat deposit overlying the sandy soil. A few bones are bored with round holes that show no indication of tool marks (Fig. 10). Some of these holes may have been made by the roots of larger plants, possibly tree seedlings. Similar perforations have been observed by the author in human burials in the eastern United States where the roots were still in place. Baker and Brothwell (1980:38) recorded comparable perforations thought to be caused by roots pushing through the cranium of a cow. These perforations are often difficult to distinguish from holes made in the ends of long bones to remove marrow. Surficial destruction from root damage was minimal, although some cutmarks were probably obliterated as a result of this process.

Erosion and weathering were the fourth and fifth most common taphonomic processes witnessed at West Row Fen. Erosion caused deterioration of the outer

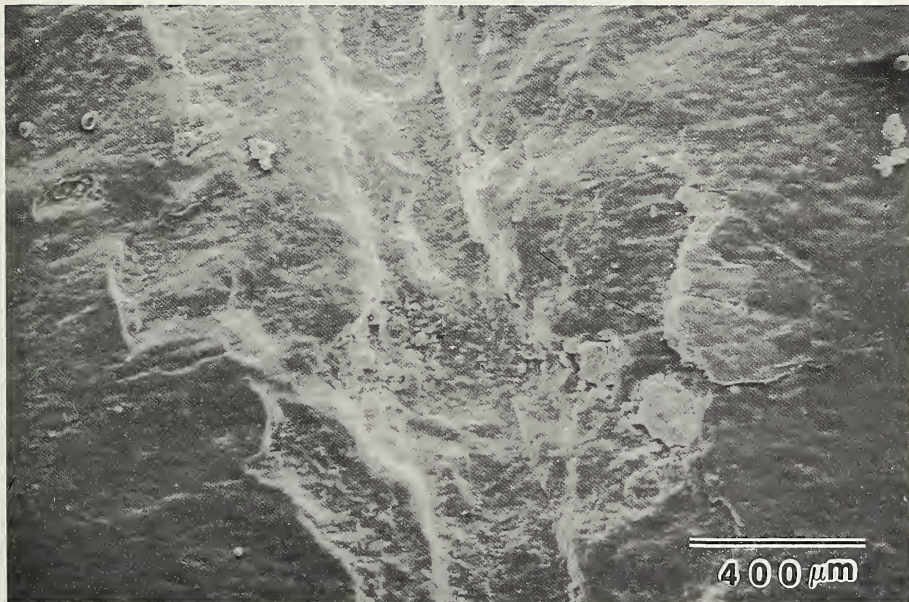


Fig. 11.—Scanning electron micrograph of a cutmark made with a dull metal knife. Note the ragged margins and unstriated, flat-bottomed groove.

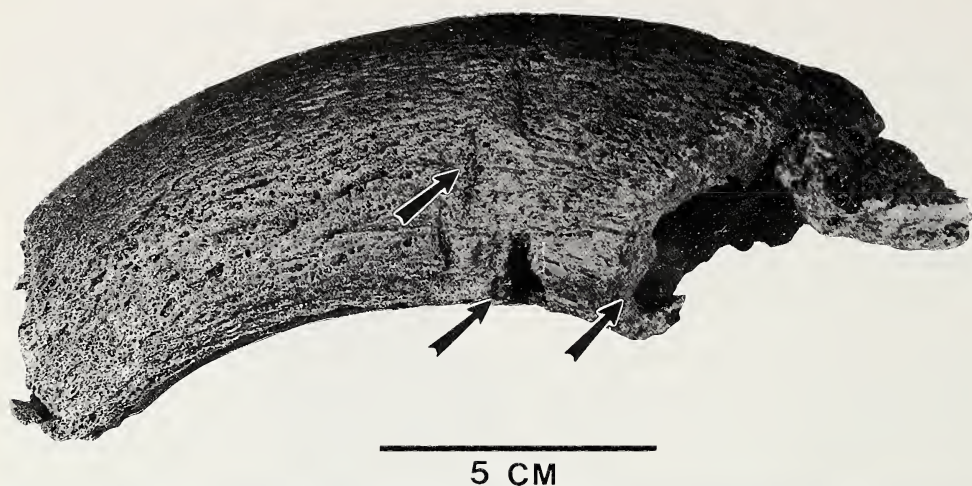


Fig. 12.—Horncore of a domestic short-horned bull with axe chopmarks around the base made during removal of the horn.

cortical bone surfaces and probably erased some evidence of cultural modification. Weathering generally resulted only in shallow surface cracks with an absence of surface exfoliation. Rodent gnawing was surprisingly rare at West Row Fen, an indication that vermin were kept to a minimum during the occupation of the village. Bones were buried relatively rapidly, and disturbance by burrowing animals was probably minimal.

BUTCHERING

Detailed descriptions and illustrations of butchering patterns accompany the discussions of most species. Bronze tools were not abundant at West Row Fen at this technological stage (E. Martin, personal communication), but there is evidence of their use in butchery. Certain criteria can reveal whether a stone or a metal tool was used to cut bone in well-preserved cases (Olsen, 1988). Most of the fine cutmarks were probably made with stone tools such as unretouched blades or flakes. These tools leave very narrow V-shaped grooves with microscopic parallel striations running along the walls of the groove (Olsen and Shipman, 1988). Metal knives, however, leave wider grooves with smoother walls and fewer parallel striations. Metal knife marks are less common than those made with stone tools, but in one example multiple cuts were made with a dull metal knife that left broad, flat-bottomed grooves with very ragged margins (Fig. 11).

Although stone butchering tools were dominant on the basis of cutmark analysis, metal axes may have been used to chop antlers and bones. The chopmark produced by a chipped stone axe is a broad, open V-shaped notch with visible macroscopic striations running down into the groove roughly perpendicular to the long axis of the mark (Olsen and Shipman, 1988). A chopmark made with a metal axe has much smoother walls, with only very faint microscopic striations. Distinguishing between chopmarks made with very thin ground stone axes and those made with metal axes is difficult, however, since both cuts have relatively smooth walls. A

Table 4.—Perforations in the ends of elements for marrow extraction.

Bag number	Taxon	Element	End perforated
0238	<i>Ovis aries</i>	radius	distal
0912	<i>Ovis/Capra</i>	radius	both
0912	<i>Ovis/Capra</i>	radius	distal
0912	<i>Ovis/Capra</i>	metacarpal	both
0912	<i>Ovis/Capra</i>	tibia	distal
0912	<i>Ovis/Capra</i>	metatarsal	proximal
0912	<i>Ovis/Capra</i>	first phalanx	proximal
0916	<i>Ovis/Capra</i>	radius	distal
0916	<i>Ovis/Capra</i>	tibia	distal
5311-II	<i>Ovis/Capra</i>	radius	proximal

few thin ground stone axes were found at West Row Fen, so it is possible that these were used to chop through bones. The West Row people apparently used either ground stone or metal axes to hack through the bases of horn cores (Fig. 12) and tough joints of cattle, as well as deer antler beams and tines.

The use of unretouched stone blades for cutting meat and metal axes for chopping through horn and bone seems to indicate efficiency. Metal axes produce greater results with fewer blows than chipped stone axes; unretouched blades are sharper, more easily obtained, and easier to manufacture than metal blades.

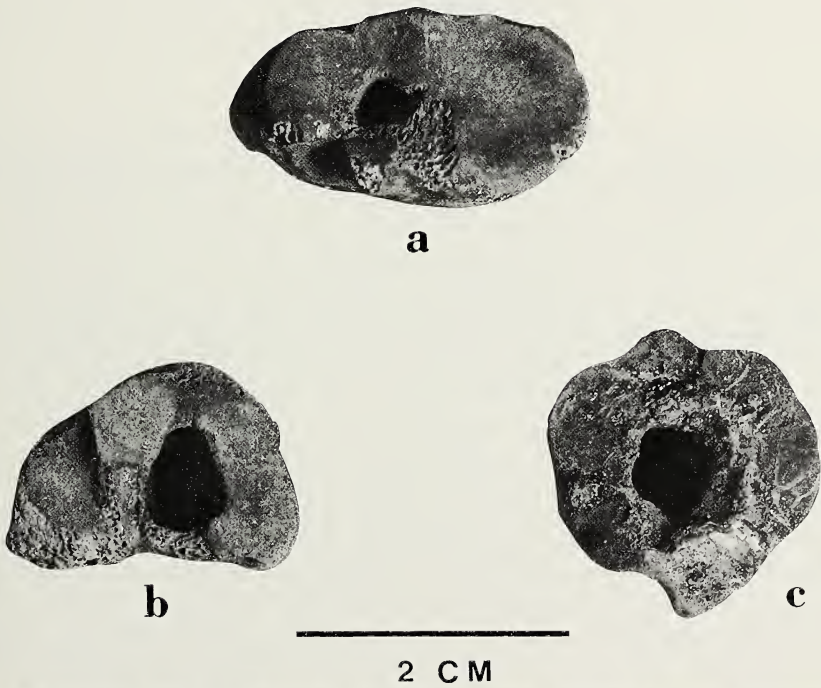


Fig. 13.—Perforations made in the ends of caprine long bones to extract marrow: a, proximal radius; b, proximal metacarpal; c, proximal metatarsal.



Fig. 14.—Posterior surface of a caprine radius with a rectangular opening for marrow extraction.

MARROW EXTRACTION

Given the intensive carnivore gnawing of long bones at West Row Fen, it is difficult to assess the frequency of marrow extraction by humans based on spiral or “green bone” fractures. There are other types of modifications that were performed by humans for this purpose, however. Long bones of sheep or goats, were perforated at one or both ends (Table 4) in order to remove the marrow. In these cases, openings were made with a gouge and then reamed or enlarged by scraping around the interior margins until they measured from 4 to 14 mm in diameter (Fig. 13). Experimentation on the articular ends of fresh bones showed that this can be done easily without leaving noticeable tool marks around the rim or wall of the perforation. In three specimens the epiphysis was removed from the diaphysis so that the soft metaphyseal material could be reamed out. In one case, the intact epiphysis was found near the perforated diaphysis in the deposit. Marrow was also extracted from a sheep or goat radius by incising a rectangular opening in the posterior surface of the diaphysis near the proximal end (Fig. 14).

Two proximal cow phalanges were opened to extract marrow from the cavity by percussion with a chipped stone hammer (Fig. 15). The two phalanges were found together and were probably derived from the same individual.



1 CM

Fig. 15.—Proximal phalanx of a domestic cow opened with a hammerstone to extract marrow (dorsal surface).

BURNING

Only five identifiable bones were found to have been burned (Table 3). Most burning does not occur during cooking, because meat is an excellent insulator, but instead takes place after the meal when the bones are discarded in the fire. Such disposal reduces the odor and unsanitary conditions caused by rotting meat and marrow, while providing some fuel for the fire. The prevalence of domestic dogs in the village (as indicated by their remains and the incidence of carnivore gnawing) may have led to the practice of throwing the bones to the dogs, rather than discarding them in the fire. Moreover, the nearby woodlands would have yielded far superior sources of fuel than that provided by bones.

PATHOLOGY

Only a few cases of pathologically altered bones or teeth were observed in this faunal assemblage. Most were congenital anomalies, healed injuries typically associated with domestication, or changes probably caused by traction. The scarcity of pathologies suggests that the domestic animal populations were healthy, but also that many individuals did not avoid culling long enough to develop serious diseases or to mend from an injury. There were no fetal and few neonatal remains recovered, but dogs may have destroyed many of these fragile bones.

THE MAMMALIAN FAUNA

Erinaceus europaeus, *Western Hedgehog*.—Three hind limb elements (a femur and two tibiae) were identified. Hedgehogs, known at least by the early Mesolithic

in Britain at the site of Thatcham, Berkshire (Davis, 1987:174), occur both in woodlands and grasslands (Corbet and Ovenden, 1980:120).

Talpa europaea, *Northern Mole*.—The fused sacrum and innominates of a northern mole were recovered from the area containing the Neolithic pits. Because of this species' habit of burrowing, the mole may have entered the site either during or after its human occupation. They presently occur in British grasslands and deciduous woodlands (Corbet and Ovenden, 1980:122).

Lepus, cf. *L. capensis*, *Brown Hare*.—Nineteen bones of hares were identified in this assemblage. Rabbits, *Oryctolagus cuniculus*, apparently did not spread through Britain until the Norman Invasion (A.D. 1066) (Corbet and Southern, 1977). The remains identified at West Row Fen have proportions comparable to *Lepus* rather than to *Oryctolagus*. *Lepus capensis* occurs in the area today, but it is possible that another species could have occupied Britain in prehistoric times (Grant, 1984). The blue hare, *L. timidus* was recorded in the early postglacial from Hartledale (Tinsley, with Grigson, 1981:218). At West Row Fen, no cranial remains were recovered and the partial mandible did not allow identification to species level. The MNI for hares is only three, but dogs could have destroyed many of the scraps left from meals of this small game.

Order Rodentia, *Genus and Species Indeterminate*.—Only a few rodents were found in the general faunal assemblage identified here. Most of the rodent elements were recovered from the sieved material and are currently being studied by T. P. O'Connor. The paucity of rodent bones may be due in part to the activities of village dogs.

?*Arvicola terrestris*, *Northern Water Vole*.—This species is normally associated with freshwater marshes, lakes, or slow-moving streams; however, it may live in grasslands away from water (Corbet and Ovenden, 1980:164). Although water voles could have been consumed by humans, it is likely that they entered the archaeological deposits intrusively at the time the peat was forming. Eleven of the 14 bones, probably all from the same immature individual, came from a single pit.

Felis sylvestris, *European Wild Cat*.—One tooth and three limb bones were recovered. These elements are difficult to distinguish from the domestic cat, *F. domesticus*, but there is no evidence that domestic cats entered Britain before the Iron Age. A cluster of kitten skeletons found at Gussage All Saints, an Iron Age site in Dorset occupied around 500 b.c. (uncalibrated), was used to establish domestication (Harcourt, 1979). The relatively large size of the radius and femur from West Row Fen supports their identification as wild cat rather than a domestic breed. Wild cats may have lurked around middens at night to catch rats and mice, although dogs would certainly have helped deter this behavior. Alternatively, wild cats may have been hunted for their fine fur to make small bags or garments.

Vulpes vulpes, *Red Fox*.—One lower jaw and nine limb bones were found strewn across a small area and could represent one adult animal. None of the bones has unfused epiphyses, and the age of fusion for the identified bones ranged from 19 to 28 weeks (Davis, 1987). Foxes might have been killed because they were pests and a threat to the young livestock, as foxes scavenge sheep and goat carcasses (Stallibrass, 1984) and could kill a newborn lamb or kid.

Two cases of butcher marks on fox bones are almost certainly the result of skinning. The first consists of several short, shallow cuts on the lateral side of the shaft of a fifth metacarpal (bag 0882) just distal to the proximal articular surface. These probably occurred when an annular incision was made around the wrist to remove the hide. The second mark was found on the anterior surface of a distal

tibia (bag 0933) and could represent an analogous cut around the ankle (Guilday et al., 1962:71). The removal of hides frequently stops short of including the strongly adhering skin of the feet and toes since this skin is of little value. Annular cuts at the wrist and ankle allow the hide to be removed in one piece, exclusive of the feet.

Canis familiaris, *Domestic Dog*.—The quantity of gnawed bones in this assemblage indicates that dogs were adept at cleaning up the food refuse produced by the village. Hunting was minimal at West Row Fen in comparison to the rearing of domestic stock, although dogs could have been trained to assist in periodic hunts. It is more likely that dogs were used to herd and protect livestock from predators such as foxes and wild cats. The dogs were medium-sized and the cranium and mandibles show characteristics of domestication such as foreshortening of the rostrum (Fig. 16). Domestic dogs are known in Britain since Mesolithic times at Star Carr (7538–7607 b.c., uncalibrated) (Degerbol, 1961).

The dentition and epiphyseal fusion data on dogs show that most of the remains preserved are from adults. The only exceptions are a mandible containing a deciduous second premolar (aged five weeks to six months; Silver, 1969) and a radius that was unfused distally (aged less than 47 weeks; Silver, 1969). One cervical, probably from an old individual, bears traces of possible osteoarthritis in the form of lipping around the cranial end of the centrum on the ventral surface.

Approximately 63% of the *Canis* material represents the skull and first two vertebrae, whereas the remaining 37% is mostly appendicular. Two atlas vertebrae (bags 5382 and 10498) have cutmarks on the ventral surfaces associated with decapitation. Diagonal marks immediately adjacent to the right anterior articular facet of one and transverse marks on the body of the other (Fig. 17) were most likely made while removing the head from the body. Another cervical (bag 4237) also bears transverse cutmarks on its dorsal surface. Deer, sheep, pigs, and cattle were also decapitated as a normal part of the butchering process at West Row Fen; therefore, no sacrificial or ceremonial inferences need to be made in the case of dogs.

The anterior surfaces of two dog radii show fine transverse cuts near the proximal ends, as does the posterior surface of a tibia. Deep cuts like these at the elbow and behind the knee suggest disarticulation of the carcass as a part of food preparation rather than skinning (Guilday et al., 1962:67). The internal surface of one rib was also butchered in a way consistent with food preparation or consumption.

Cunliffe (1991) reported a high frequency of butchered dog bones at the Iron Age site of Highfield. At West Row Fen, the lack of dog burials, the presence of butchering marks, the scattering of their bones throughout the site, the deposition of a partial skeleton and isolated bones in refuse pits (Table 1), and the occurrence of one spirally-fractured and one burnt dog bone suggest that these animals were probably eaten and were not particularly revered as pets.

Capreolus capreolus, *Roe Deer*.—Roe deer were present in Britain intermittently during the Pleistocene interstadials and continuously after the Preboreal (ca. 8300 b.c.), when forests replaced grasslands. They appear in prehistoric sites in or near forests from the Mesolithic on, but their numbers generally decline in the Neolithic as domestic stock becomes increasingly more important (Grigson, 1984).

At West Row Fen, roe deer element frequencies do not vary dramatically, which is compatible with the idea that these small animals were probably carried into the site whole. The sample is too small to construct a mortality pattern, but epiphyseal fusion and dental evidence show that adults were taken more frequently than juveniles. Roe deer would have provided about the same amount of meat

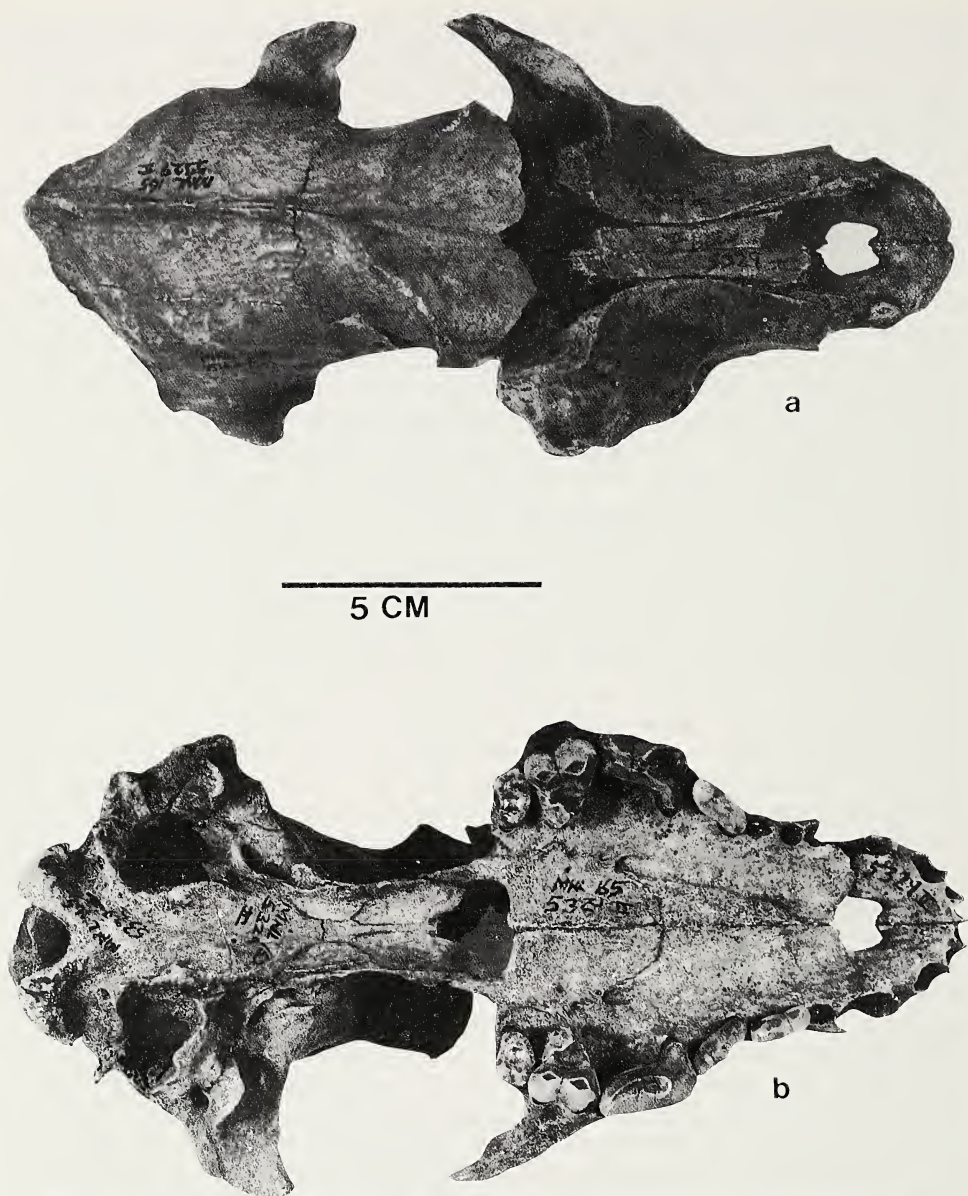


Fig. 16.—Domestic dog cranium from West Row Fen: a, dorsal view; b, basicranial view.

as the small Soay sheep, but, as wild game, would not have yielded milk and wool. Roe deer rank seventh at West Row in the amount of contributed meat (Table 2).

Roe deer antlers, because of their small size, spatulate shape, thin cortical layer, and predominantly spongy interior, were much less useful for manufacturing artifacts than were the antlers of red deer. As far as can be discerned, all of the

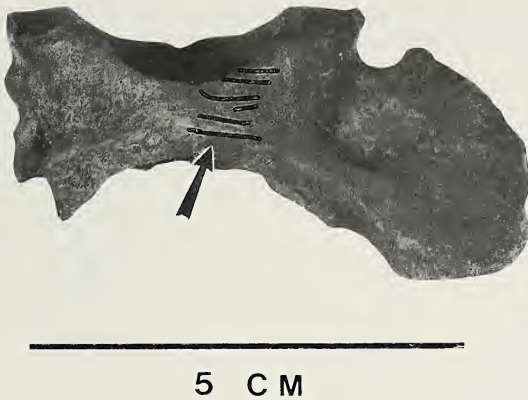


Fig. 17.—Ventral view of a dog atlas, illustrating locations of cutmarks.

worked antlers from West Row Fen are derived from red deer. One of the unmodified roe deer antlers, however, was collected after it was cast by the deer.

Cutmarks on the medial shaft of one roe deer metacarpal imply skinning. The distal epicondyle of a humerus bears several annular cutmarks, like those usually associated with the removal of the forearm flexors and extensors. Two astragali and one calcaneus exhibit transverse cuts that represent disarticulation of the ankle. All of these are common butcher marks made in the preparation of a medium or large mammal for consumption.

Cervus elaphus, Red Deer.—Red deer have a paleontological distribution pattern similar to that of roe deer—flourishing in the Pleistocene interstadials and returning with the forests of the Holocene. They, too, have been identified in sites that date back to the Preboreal (Davis, 1987). At West Row Fen, red deer remains were more plentiful than those of roe deer according to their NISP, but less common in their MNIs. Red deer yield about nine times as much meat as roe deer, however, and have antlers that are far more useful for manufacturing artifacts. By weight of usable meat, the red deer is the third most important species consumed at West Row Fen.

The one definite piece of seasonality information comes from an antler still attached to the frontal bone (bag 5349) of a deer that was killed between September and March. Four red deer antlers were chopped through the beam just above the pedicle, suggesting that they were cut from the frontal during butchering. The most remarkable of these was found in Pit 4284 and is 42 cm long. It had been split in half longitudinally by chopping with a metal axe in preparation for artifact manufacture. Three cast antlers demonstrate the apparent need at West Row Fen to gather this valuable raw material for artifact manufacture. Two of the cast antlers were made into mace-heads. Additional antler artifacts include four rod-like flakers, eight modified tines, a wedge, and a hollow handle.

That red deer provided meat and hides as well as antlers for making artifacts is evident from the butchering patterns. The atlas of one red deer bears several long cutmarks on the ventral surface reflecting decapitation. The anteromedial surfaces of two radii exhibit fine cuts near the proximal ends, inflicted when the elbow joint was disarticulated. Finally, a proximal phalanx was cut on the side just above the distal condyle during skinning.

Table 5.—*Survival based on epiphyseal fusion for Sus scrofa. Ages of fusion based on Silver, 1969:252–253.*

Age in months	Element	End ^a	Unfused		Fused		% Surviving ^b
			Left	Right	Left	Right	
12	humerus	D	4	2	2	4	50
12	radius	P	1	0	2	2	80
24	tibia	D	0	1	1	5	86
42	femur	P	1	2	0	0	0
42	radius	D	2	1	0	0	0
42	tibia	P	0	5	0	0	0
42	femur	D	2	2	0	0	0
42	humerus	P	2	0	0	0	0

^a P = proximal, D = distal.

^b Surviving beyond age of fusion.

All red deer bones retaining epiphyseal areas are fused. Identified teeth include one left and right deciduous premolar and 28 permanent cheek teeth. There is little evidence that juvenile red deer were hunted with any frequency.

Sus scrofa, *Pig*.—Wild boars, like the roe and red deer, invaded Britain once the forests began to dominate and were present from the Preboreal onward. The earliest evidence for small, apparently domestic, pigs is derived from the Neolithic causewayed camp at Windmill Hill (ca. 2960 b.c., uncalibrated; Davis, 1987:177).

Osteological features alone do not reveal whether wild boars were hunted occasionally by West Row people. Two large adult pig bones—a temporal and an ulna—were recovered, but since fully adult domestic pig bones are rare in this collection, the maximum size of a typical domestic male cannot be estimated. Milisauskas (1978:67) estimates a significant difference between the amount of usable meat produced by an average wild boar (53.75 kg) compared to an early domestic pig (15 kg).

Most of the fused epiphyses were those that fuse at birth or within the first two years of life (Table 5). Those that fuse between 2 and 3.5 years were always unfused. The quantity of immature bones argues that most, if not all, of the pigs at West Row Fen were domesticated and that culling of young individuals occurred.

Based on the teeth (Table 6), a slightly different picture of the age structure of pigs at West Row Fen emerges. Bull and Payne (1982) demonstrated that there are only minor differences between wild boars and modern domestic pigs in the timing of tooth eruption and epiphyseal fusion. Therefore, the age categories for wild boars have been applied to the dentition of Early Bronze Age domestic pigs. Wild boars mature only slightly quicker than modern domestic pigs, which have undergone far more artificial selection than the Bronze Age pigs. The dental evidence from West Row Fen shows that at least some individuals survived long enough to reach full size. Based on the right mandibles, the most common jaws in the assemblage, 45% of the pigs were being killed in the first 16 months of life. Another 36% died between 19 and 35 months, and 18% survived to about four years or beyond. This pattern suggests that while the mortality rate was heavy in the first year, at least some pigs were reserved for breeding and were kept to grow until they were needed for their meat. It was uncommon, however, for a pig to survive beyond three years.

The average dressed weight of a mature European wild boar is about 36.4 kg, but it is just 13.6 kg for a wild piglet (Henry, 1969; Biddick, 1984:165). Assuming comparable ratios for early domestic pigs in Britain, the mortality patterns bear

Table 6.—Age distribution of *Sus scrofa* based on mandibles with two or more teeth. Aging of dentition done by using Silver (1969) for dates of eruption and Bull and Payne (1982) for wear stages.

Age category	Left	Right
1 week to 16 months	1	
7 weeks to 16 months	2	
4 months to 16 months	1	2
7 months to 16 months	2	1
8 months to 16 months	1	
19 months to 23 months	1	3
19 months to 35 months	1	
31 months to 35 months	3	1
Over 35 months		2
Total	12	9

on the relative importance of pork in the diet of the West Row people. Although some individuals were kept to adulthood, most were slaughtered before full growth had been achieved. This would considerably lower their relative dietary contribution compared to cattle and red deer, which were primarily slaughtered as adults. However, pork has a higher caloric value than beef, venison, or mutton. Per kilogram, mutton provides 1500 calories; beef, 2000 calories; and pork, 3700 calories (Flannery, 1969). If calories are considered over pure units of meat weight, pigs would again increase in relative value, although their caloric value would depend in part on whether juveniles have the same proportion of fat as adults.

Butchering marks are not very common on pig bones (Fig. 18; Table 7) except on the distal epicondyles of humeri. Marks on a lacrimal and on the lingual surface of a mandible (not figured) illustrate that skin and meat were removed from the head. One occipital bears traces of decapitation. Cutmarks on a scapula, humeri, an innominate, and a femur were probably made while removing meat and disarticulating the joints. Ribs were cut away from the vertebrae in the process of disarticulating the carcass. Ribs were also scraped on the internal surfaces probably during human consumption of the intercostal muscles. Removal of the hock is indicated by cuts on the astragalus, calcaneus, and navicular bones. One pubis (not figured) bears a cut probably made while skinning or eviscerating the animal.

Live pigs do not produce useful products such as wool and milk, although their manure may be used for fuel or fertilizer. One possible benefit of raising pigs is that they root up the soil thus serving the same function as a plow (Reynolds, 1976).

Although they may have been supplied with grain and legumes occasionally, pigs could have survived primarily on garbage and pannage provided by nearby forests. Grass and bracken would have been available locally in the spring and summer. Stubble left in pastures grazed by sheep and cattle was another possible food source for swine. If pigs were kept primarily for their meat and lard, their numbers would probably have been maintained below the level that would require much provisioning with grain that people could have consumed. Though pigs are inexpensive to feed, if their numbers get too large, they begin to become a nuisance. Too many pigs are difficult to manage because they tend to get into gardens and destroy food intended for people (Rappaport, 1968). Because a female produces eight to ten piglets at a time (Towne and Wentworth, 1950:253), some culling would be necessary to prevent overpopulation.

*Ovis aries/Capra hirc*a, *Domestic Sheep or Goat*. —Sheep and goats were brought

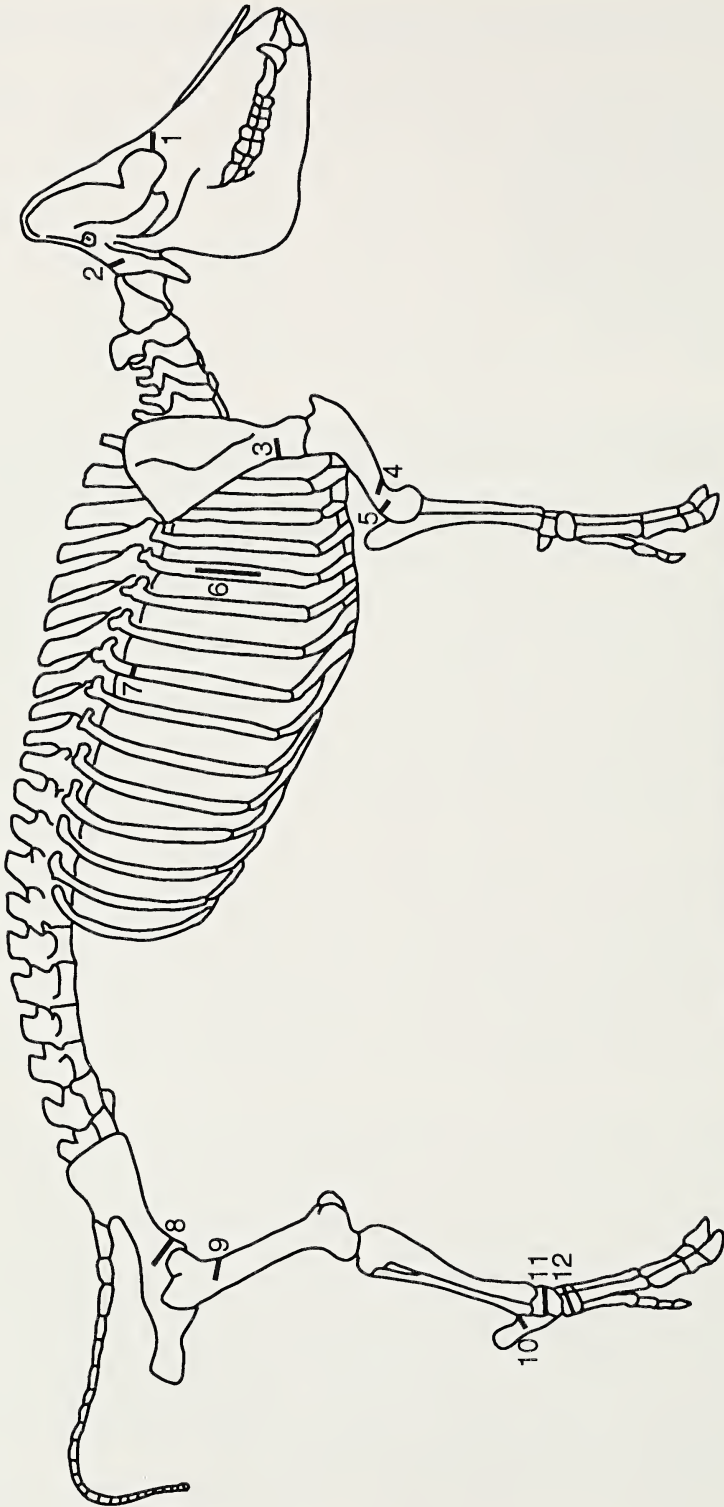


Fig. 18.—Distribution of butcher marks on pig bones.

Table 7.—Key to butchering patterns for *Sus scrofa*.

Location and type	Number of bones cut
1. Skinning	1
2. Decapitation	1
3. Disarticulation of shoulder	1
4. Muscle removal	2
5. Disarticulation of elbow joint	2
6. Muscle removal	2
7. Segmentation of thorax	2
8. Disarticulation of hip	1
9. Muscle removal	1
10. Severing Achilles tendon	1
11. Disarticulation of ankle	2
12. Disarticulation of ankle	1

into Britain across the English Channel during the Neolithic (Ryder, 1983:64–65) and increased in numbers compared to other livestock in the Bronze Age as the forests diminished (Trow-Smith, 1957). By NISP, caprines were second in frequency to cattle at West Row Fen, but the MNI for caprines was higher than for cattle (Table 2). Since it takes the meat of 28 sheep or goats to match that of a cow, however, it is clear that far more pounds of beef were produced in the village than mutton or goat meat.

Of the six bones identified as those of domestic goats, three were horn cores. The breed of these goats is not discernable; they appear to have been small and gracile like the sheep, but are far less common. Sheep thrive much better in cool, wet lowland farming communities, whereas goats prefer hotter, more arid climates (Redding, 1984:237) and rugged terrain. According to Grant (1984), sheep were also much more plentiful than goats during the Iron Age in Britain. Mixed herds of sheep and goats are common among livestock herders, partly because goats are thought to improve herd management and to provide leadership for the sheep, although this has never been scientifically documented (Redding, 1984:29).

The sheep from West Row Fen were small, slender-limbed, two-horned individuals that are within the size range of the Soay breed. According to Reynolds (1987), Soay sheep probably developed as a breed during the Bronze Age and were common until the Iron Age, when four-horned breeds like the Hebridian and Manx Loghtan breeds arose.

Because of their fragmentary nature, most of the bones in this size range could only be identified as caprines (*Ovis aries/Capra hircus*). Although the better preserved material hints that sheep considerably outnumbered goats, we cannot make that assumption for the bulk of the less-identifiable material.

Survival patterns reflected by epiphyseal fusion for *Ovis/Capra* indicate that there was a serious drop in the proportion of individuals living beyond the first year (Table 8). At ten months, over 90% were still alive, but by 13 months only half to a third remained. By 3 to 3.5 years, only a third to a quarter survived. This pattern is similar to the one seen in the pig dentition records and suggests that culling of young individuals took place. In this case, the reason for killing juveniles is probably more than just a desire for the meat, although lamb is preferable to mutton. Cultures relying on sheep and goat dairy products need to kill enough of the young to have a surplus of milk for human consumption (Davis,

Table 8.—*Survival based on epiphyseal fusion for Ovis aries/Capra hirca. Ages of fusion based on Silver, 1969:252–253, except for phalanges. At West Row the proximal epiphyses fused **after** the distal epiphyses in cattle and caprines, counter to Silver.*

Age in months	Element	End ^a	Unfused		Fused		% Surviving ^b
			Left	Right	Left	Right	
10	humerus	D	1	0	15	19	97
10	radius	P	2	1	17	19	92
13–16?	phalanx 1	P	8	3	3	10	54
13–16?	phalanx 2	P	2	4	7	4	65
18–24	tibia	D	7	5	10	11	64
18–24	metacarpal	D	4	5	1	1	18
20–28	metatarsal	D	4	2	2	3	45
30–36	femur	P	6	6	0	3	20
36	radius	D	12	12	5	5	29
36–42	tibia	P	4	5	1	2	25
36–42	femur	D	4	5	3	2	36
36–42	humerus	P	3	4	1	3	36

^a P = proximal, D = distal.

^b Surviving beyond age of fusion.

1987:180; Legge, 1992). Males are usually killed in their first year, leaving only enough to breed with the females. Many of the females are allowed to mature beyond the age of two or three years in order to reproduce and yield milk.

Determined age categories based on caprine mandibles (Table 9) are quite broad and do not often coincide because tooth rows and comparable teeth are poorly preserved from one mandible to the next. Most mandibles preserve only two or occasionally three teeth, but molar alveoli provided additional evidence for aging jaws. Despite these constraints, the data indicate that at least two individuals were killed between the ages of two and three months. Nineteen died before they were two years of age; eight survived past the age of three years, seven of those past 5.5 years, and one beyond eight years. This evidence indicates that many indi-

Table 9.—*Age distribution of Ovis aries/Capra hirca based on mandibles with two or more teeth. Age based on Silver (1969) and Legge (1992).*

Age in months	Left	Right
1–24		2
2–3		2
3	1	
>3	1	
3–10	1	
3–24	2	7
9–12	3	
>18		1
18–24		1
<24	4	5
>21	2	4
21–24		2
21–34	1	
10–65		1
34–65	1	1
65–100	5	6
>100	1	
Total	22	32

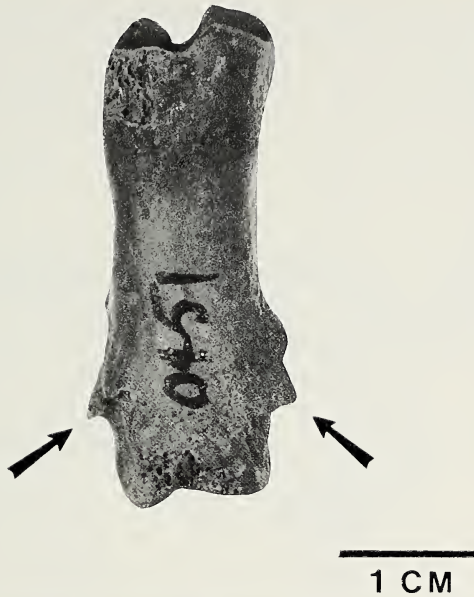


Fig. 19.—Pathological exostosis on a proximal phalanx of a caprine. Arrows point to abnormal flanges of bone on both sides.

viduals were being maintained well beyond the age when mature weight is achieved, which suggests that their primary function was dairy production rather than meat provisioning. The scant dental data do not reveal whether very young lambs and kids were regularly culled, as would be expected if people were utilizing dairy products.

Unfortunately, there is no evidence for the use of sheep wool at West Row Fen, since no textiles or antler combs suitable for plucking fleece have been found at the site. Sheep shears are not known until Roman times (Reynolds, 1987). However, Bronze Age textiles made from Soay-type wool have been found in England (Ryder, 1983:47). A sample from Rylston, in Yorkshire, consists of a piece of yarn made of fine fibers associated with pieces of a generalized medium and a hairy medium wool (Ryder, 1969).

The only pathology among the caprine bones is a proximal phalanx that has indentations on both sides of the distal epicondyle with lipping above (Fig. 19). The unusual symmetry of these injuries suggests that they may have been induced by a human-made trap or a hobble.

Butcher marks are fairly common on the bones of caprines at West Row Fen (Fig. 20; Table 10). In contrast to the West Row cattle, the horn cores and frontals of sheep and goats do not exhibit chopmarks or cutmarks indicative of the use of their horns as a raw material. Only one chopmark was observed on a caprine bone, in contrast to many on bones of cattle. Skinning marks were found on the maxilla, anterior surfaces of the metapodials, and proximal phalanges of caprines. One hyoid bore traces of cutmarks made when the tongue was removed. The heads of sheep were removed by cutting between the occipital and the atlas, leaving small cutmarks on an occipital and both dorsal and ventral surfaces of an atlas. Disarticulation cuts were found on caprine cervical vertebrae; at the shoulder on

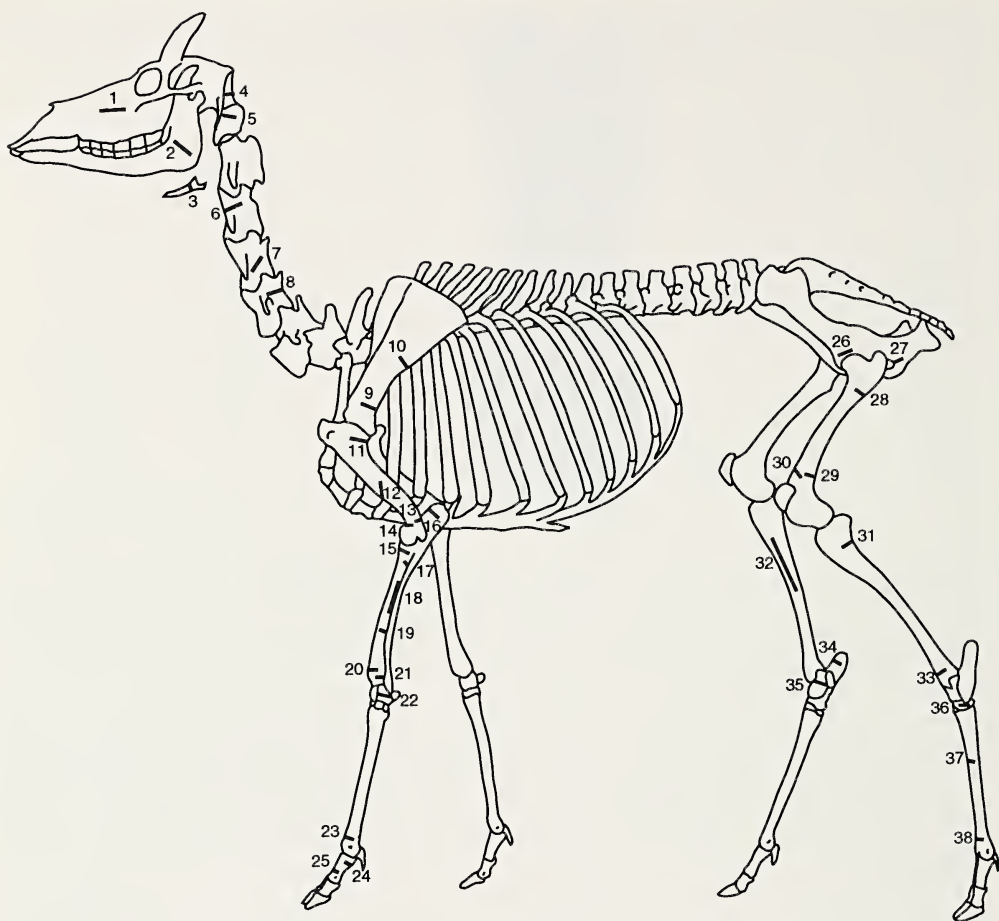


Fig. 20.—Distribution of butcher marks on caprine bones.

the scapular neck and humeral head; the elbow joint on the humerus, radius, and ulna; the distal radius and the scaphoid of the wrist; above the acetabulum of the innominate; and at the ankle on the astragalus, navicular, and calcaneus. Some filleting and other types of meat removal are indicated by midshaft cuts or scraping on the scapula, humerus, radius, femur, and tibia.

To determine how the vertebrae and ribs were butchered, it is necessary to examine the bones that could only be identified as small ruminants, since it is difficult to distinguish among fragments from sheep, goats, and roe deer. These show minor cutmarks on the neural spines of the thoracic vertebrae, a chopmark completely through a thoracic centrum and neural arch (probably with a metal axe), disarticulation of the ribs and vertebrae at the rib's head and tubercle, and scraping of the internal surface of the rib. All of these cutmarks are commonly found on carcasses butchered for food consumption.

Bos primigenius, *Wild Aurochs*.—Most of the *Bos* remains represent domestic cattle. Although a few of the elements are large, only one is attributable to the wild aurochs—a distal humerus with a trochlear breadth of 9.9 cm and proportions comparable to that of a bison.

Table 10.—Key to butchering patterns for Ovis/Capra.

Location and type	Number of bones		
	Cut	Chopped	Scraped
1. Skinning	1		
2. Muscle removal	1		
3. Tongue removal	1		
4. Decapitation	1		
5. Decapitation	1		
6. Segmentation of neck	1		
7. Segmentation of neck	1		
8. Segmentation of neck	1		
9. Disarticulating shoulder	2		
10. Muscle removal	1		
11. Disarticulating shoulder	1		
12. Muscle removal	1		
13. Disarticulating elbow	1		
14. Disarticulating elbow	13		
15. Disarticulating elbow	10		
16. Disarticulating elbow	16		
17. Disarticulating elbow	2		
18. Fileting upper forelimb			1
19. Fileting upper forelimb	1		
20. Disarticulating wrist	1	1	
21. Disarticulating wrist	3		
22. Disarticulating wrist	1		
23. Skinning, tendon removal, or disarticulating of joint	1		
24. Same as 23	1		
25. Same as 23	1		
26. Disarticulating hip	1		
27. Eviscerating or skinning	1		
28. Muscle removal	3		
29. Muscle removal	2		
30. Muscle removal	1		
31. Muscle removal	1		
32. Fileting lower leg			1
33. Disarticulating ankle	1		
34. Severing Achilles tendon	1		
35. Disarticulating ankle	3		
36. Disarticulating ankle	2		
37. Skinning	2		
38. Skinning, tendon removal, or disarticulation of metatarsal- phalangeal joint	1		1

The wild aurochs appears to have become extinct in Britain during the Bronze Age (Tinsley, with Grigson, 1981), but its remains have been identified in mixed Beaker and Early Bronze Age deposits at Snail Down; Early Bronze Age levels at Lowes Farm near Littleport, Cambridgeshire; and at nearby County Farm, Mildenhall Fen (Tinsley, with Grigson, 1981:219). A whole skeleton was recovered from Early Bronze Age levels at Charterhouse Warren Farm, Blagdon, in Somerset (1295 b.c., uncalibrated or 1629 B.C., calibrated—Everton, 1975; Clutton-Brock and Burleigh, 1983).

Bos taurus, Domestic Cattle.—Cattle are well-suited to the lowlands of the fens, where water is in good supply. They can be used for draft, and yield dairy products, meat, large hides, bones, and horn. However, cattle require considerable pasture

Table 11.—*Survival based on epiphyseal fusion for Bos taurus. Ages of fusion based on Silver (1969), except for phalanges. At West Row the proximal epiphyses fused after the distal epiphyses in cattle and caprines, counter to Silver.*

Age in months	Element	End ^a	Unfused		Fused		% Surviving ^b
			Left	Right	Left	Right	
12–18	humerus	D	0	1	20	14	97
12–18	radius	P	3	1	24	20	92
18?	phalanx 1	P	4	2	21	21	87
18?	phalanx 2	P	5	1	27	9	86
24–30	tibia	D	1	2	18	20	93
24–30	metacarpal	D	3	4	6	5	61
27–36	metatarsal	D	1	0	8	7	94
42	femur	P	2	0	1	2	60
42–48	radius	D	1	6	4	3	50
42–48	tibia	P	0	1	4	5	90
42–48	humerus	P	1	1	2	1	60

^a P = proximal, D = distal.

^b Surviving beyond age of fusion.

and keeping them reduces the mobility of their owners, which means less opportunity to move to fresh pastures as needed.

The Bronze Age witnessed the development or arrival of a small, short-horned variety of cattle in Britain, which was apparently represented at West Row Fen. The two most-complete horn cores have basal circumferences (180 and 195 mm) well within the range of either Neolithic domestic males or wild females, but the reconstructed length of the outer curvature (roughly 200 to 250 mm) is only about half that for Neolithic domestic males and wild females (Grigson, 1982), suggesting that they were derived from domestic short-horned males.

At West Row Fen, most of the limb bones of domestic cattle are very slender, but few could be measured due to their comminuted state and the extent of carnivore gnawing on condyles. With the exception of the enormous aurochs humerus, the few large specimens may represent the limited number of intact bullocks allowed to reach adulthood. The data from the epiphyseal fusion of cattle long bones (Table 11) indicate that most individuals survived past the age when full growth was obtained. The 90% representation of fused distal tibiae may be an accident of preservation, but it still appears that over 50% of the cattle survived beyond 3.5 years of age. Immature bones are less likely to be preserved, given the activity of dogs and sedimentary abrasion from trampling. However, proportionally far more immature caprine and pig bones are preserved in the assemblage, and they are smaller and more fragile than those of immature cattle.

Cattle mandibles are only slightly better preserved than those of caprines. For the most part, they contain only two to three teeth, and no complete tooth rows are preserved. The largest age group represented by mandibles (Table 12) is in the six- to eight-year bracket and there are more minimum numbers of individuals in the full adult categories than for young juveniles. The age distribution does not imply culling of individuals in the first year of life, suggesting that cattle were kept primarily for meat and draft rather than for their dairy products (Legge, 1992). The high number of survivors beyond six years also argues in favor of their use for pulling plows and carts.

Several pathologies and anomalies were noted on cattle teeth and bones. The mandible of an individual over 28 months in age (bag 0901) shows the absence of the second permanent premolar, with no sign of infection or injury. The absence

Table 12.—*Age distribution of Bos taurus based on mandibles with two or more teeth. Age based on Legge, 1992.*

Age in months	Left	Right	MNI	% of total MNI
<1			0	0
1–3		1	1	5
3–6		1	1	5
6–15	2	1	2	11
15–26	2		2	11
26–36	2	3	3	17
36–72		4	4	22
72–96	5	1	5	28
Total	11	11	18	

of teeth is an anomaly found in many domestic species, including cattle (Baker and Brothwell, 1980:137). Another mandible of an individual older than 24 months (bag 5285-II) exhibits malocclusion and unusual wear patterns. An isolated third lower molar (bag 0297) is worn in an uncharacteristically jagged pattern, apparently from malocclusion. A smaller than usual postzygopophysis, apparently a congenital anomaly, occurs on one thoracic vertebra (bag 0418). Exostosis associated with either an injury or osteoarthritis caused lipping of the semilunar notch on one adult ulna (bag 5279-II). Baker and Brothwell (1980:115) reported a similar pathology from the site of Crandon Bridge.

Importantly, one innominate (bag 5285-II) has a swelling on the ischium involving the acetabular rim and the area just lateral to it (Fig. 21). Baker and Brothwell (1980) reported osteoarthritis on a bovine acetabulum from the Mote of Mark, and Baker has observed many examples of eburnation of the acetabulum of cattle from Roman to Medieval deposits at Winchester (Brothwell, 1981). These pathologies have been interpreted as representing excessive strain on the hip joints due to an activity that leads to overrotation of the femoral head, such as pulling a plow or a heavy cart.

Two adult proximal phalanges of cattle (bags 5101-II and 5118-II) show a heavy development of the tuberosities on the volar surface (Fig. 22), which may indicate that these animals were used for draft. The palmar (plantar in the hind foot) annular ligament spans over the tendons of the digital flexors (Getty, 1975:858–59), binding them against the bone, and attaches to the tuberosities on the volar surface of the proximal phalanx. Heavily developed tuberosities could indicate greater than usual stress on these flexor tendons, which insert on the mesial and distal phalanges. Exostosis development in third phalanges related to stress at the point of insertion for the flexor tendons has been associated with plowing in water buffalo and cattle (Higham et al., 1981).

The pathologies of cattle bones and teeth from West Row Fen are those often associated with domestication. Malocclusion and the anomalous absence of teeth are frequently related to genetic changes brought about by breeding, like the foreshortening of the rostrum. Exostosis caused by injury, strain, or old age is more common in domestic animals because they are provisioned and protected despite their impaired movement. The exostosis on the ulna could have been caused by the additional stress placed on the elbow joint while plowing or pulling heavy loads. Pathologies of the bones of the hips and feet in European prehistoric domestic cattle are more common than those seen in sheep and pig remains, and



Fig. 21.—Innominate of *Bos taurus* exhibiting a swelling on the ischium involving the acetabular rim and area lateral to it: a, anterior view; b, lateral view.

have been attributed to the impact of stress and strain in cattle due to their use for draft (Baker and Brothwell 1980:117).

The butchering patterns for cattle (Fig. 23, Table 13) are similar to those for sheep and goats with two exceptions. Horn cores and the frontal bones around the cores were often chopped with an axe when removing the horn (Fig. 12). These numerous, heavy marks demonstrate that cow horn was a valued resource for the manufacture of artifacts or glue.

The second difference involves the frequency of heavy chopping compared to fine cutmarks. Chopmarks are rare on the bones of small ungulates, but are much more common on the elements of cattle, which reflects the thicker ligaments and tendons as well as the heavier bones found in cattle.

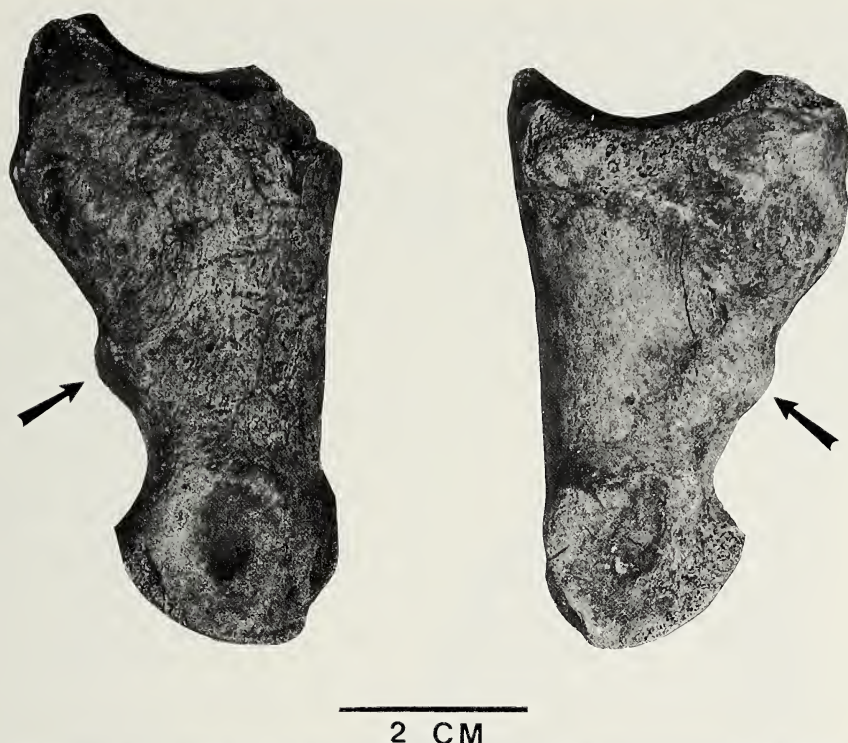


Fig. 22.—Proximal phalanges of oxen showing hypertrophy of the tuberosities for the palmar (or plantar) annular ligament, perhaps resulting from strain inflicted on the digital flexors during plowing or while pulling a heavy cart.

Possible skinning marks occur on the nasal, maxilla, and mandible, as well as on a metacarpal, and first and second phalanges. One hyoid bone bears two cutmarks made during removal of the tongue. Both atlas and axis vertebrae exhibit signs of butchery associated with decapitation. Disarticulation cuts were made between cervical vertebrae in the neck, on the mandible and malar to remove the lower jaw, and at the shoulder, elbow, wrist, hip, and ankle. Meat was removed from the bone of the mandible, scapula, humerus, radius, innominate, femur, and tibia. The most thorough fileting was performed on scapulae, which were often scraped on both surfaces and along the spine. The attention given to this element suggests that the shoulder roast was one of the most preferred cuts of meat. Ribs of large ungulates (probably cattle) were disarticulated from the vertebrae, leaving cutmarks or chopmarks on the rib heads and tubercles.

Cattle at West Row Fen were used for meat and draft, based on evidence from their butchery, mortality pattern, and pathologies. In terms of the quantity of identified specimens and meat poundage, cattle outrank all other species of animals consumed by the people at West Row Fen. The mortality pattern does not suggest that cattle were kept primarily for their dairy products, although it is unlikely that this resource was completely overlooked. Cow horn was an important by-product, judging from the number of chopped horn cores and frontals.

Equus caballus, *Horse*.—Wild horses inhabited Britain throughout the Pleistocene and into the Holocene, but never crossed over to Ireland. Small numbers

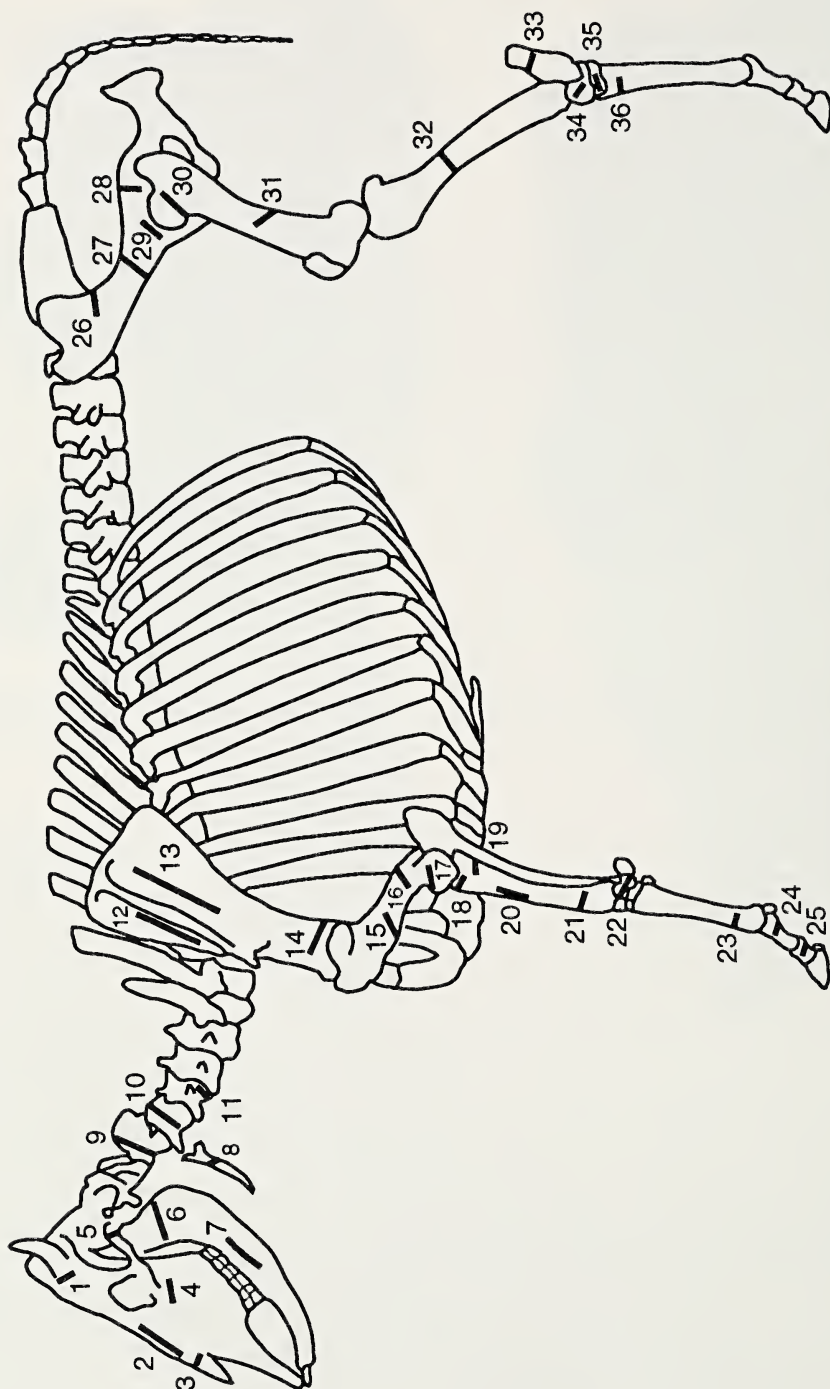


Fig. 23.—Distribution of butcher marks on cattle bones.

Table 13.—*Key to butchering patterns for Bos taurus.*

Location and type	Number of bones		
	Cut	Chopped	Scraped
1. Horn removal		7	
2. Skinning	2		
3. Skinning	3	1	
4. Skinning	2		
5. Disarticulating mandible	3	1	
6. Muscle removal	8		
7. Skinning	4		1
8. Tongue removal	1		
9. Decapitation	2		
10. Decapitation		2	
11. Segmenting neck	2	3	
12. Fileting shoulder			3
13. Fileting shoulder			1
14. Disarticulating shoulder	4	4	2
15. Muscle removal	1		
16. Muscle removal	1		
17. Disarticulating elbow	8		
18. Disarticulating elbow	8		
19. Disarticulating elbow	1		
20. Fileting upper forelimb	1		
21. Disarticulating wrist	1		
22. Disarticulating wrist	2		
23. Skinning	1		
24. Skinning, tendon removal, or disarticulating joint	4		
25. Same as 24	1		
26. Muscle removal	2		
27. Segmenting pelvis	1		
28. Disarticulating hip	2		
29. Disarticulating hip	3		
30. Disarticulating hip	2		
31. Muscle removal	1		
32. Muscle removal	1	1	
33. Severing Achilles tendon	2		
34. Disarticulating ankle	6		
35. Disarticulating ankle	4		
36. Disarticulating ankle	2		
Not shown: Marks on subspinous fossa of scapula from fileting shoulder	17		

of horse remains have been found in Mesolithic, Neolithic, and Early Bronze Age sites in Britain. It is unclear how early domestic horses arrived in Britain, but evidence at Newgrange, in Ireland, demonstrates that they were introduced there by the time of the Beaker Culture (Wijngaarden-Bakker, 1974). Whether these early domestic horses were ridden is unknown, because bronze mouth bits and antler cheek pieces from harnesses do not appear until the Late Bronze Age at sites such as Runnymede in Britain (Longley, 1980) and Newgrange in Ireland (Burgess, 1974). Based on the scant osteological evidence, it is not possible to say whether the horses from West Row Fen were wild or domesticated.

Just seven teeth and eight bone fragments were identified as horse. Two of the teeth are deciduous premolars and one cervical is unfused at the caudal epiphyseal

plate, representing the remains of at least one immature horse. The other teeth (a worn lower third incisor and a lower third molar) belong to an adult.

The distal epicondyle of an adult horse metapodial was butchered. Multiple transverse cuts on either the medial or lateral surface of this bone are probably indicative of skinning rather than disarticulation, because they are well above the joint. There is no evidence that horses were eaten at West Row Fen, but the single butchered bone suggests that their hides may have been utilized.

BONE AND ANTLER ARTIFACTS

Of the collection of 120 bone and antler artifacts recovered from West Row Fen, 76 are bone awls made from sheep or goat bones. Twelve of these are drilled near the base for sewing or for suspension. A pin, a scoop, and a spatula have also been identified. Ornaments are restricted to three simple, undecorated tubular beads. The most spectacular piece is a well-made and finely polished bone dagger with a tanged handle that may have been a skeuomorph of a more effective bronze weapon.

Many of the artifacts were made from red deer antler, an apparently plentiful and useful raw material. Of the twelve pressure flakers recovered, eight were modified tines, and four were rods cut from antler beams by grooving-and-snapping. A hollow antler handle with two rivet holes and two socketed mace-heads provide clues about how pieces of composite tools were attached to one another. A single antler wedge may have been used in conjunction with an antler mace-head to split wood.

Eighteen pieces of debitage helped decipher manufacturing techniques. These include a split antler (42 cm long) from the soaking pit, a severed antler tine, nine grooved-and-snapped ruminant metapodials, as well as other small indeterminate fragments bearing manufacturing traces.

CONCLUSIONS

West Row Fen fits into and generally supports a trend seen in smaller British faunal assemblages from the Neolithic through the Iron Age. During the Early Neolithic (ca. 3500 B.C. to 2750 B.C.), the Windmill Hill culture on the Salisbury Plain depended primarily on cattle (70%), followed by pigs (17%) and sheep/goats (13%) (Ryder, 1983:65). In the Late Neolithic, cattle and pigs occur most frequently in the archaeological record. Sheep and goats were still fairly rare. Cattle began to outnumber pigs in Beaker sites and were prevalent throughout the Bronze Age. From the Early Bronze Age, sheep and goats increased and pigs declined in numbers (Tinsley, with Grigson, 1981). Ryder (1983:72-73) attributes this to the clearing of woodlands.

The Bronze Age of Britain took place during the Subboreal period, which was marked by a decrease in precipitation that reduced productivity in farming and regeneration of forests, but improved conditions for pastoralism in low-lying, poorly drained areas (Ryder, 1983:72-73) such as the fens of East Anglia. This increase in pastoralism is probably responsible for the scarcity of Bronze Age settlement sites in Britain, because nomadism would also have increased. Because of the paucity of large Bronze Age sites, little is known of the relative frequencies of domestic animals and wild game during this period. West Row Fen demonstrates the rise of importance of caprines and the decline of pigs during the Early Bronze Age.

West Row Fen is dominated by cattle in terms of number of bone fragments and estimated meat poundage, but the minimum number of individuals for caprines (sheep/goat) is higher than for cattle (Table 2). Pigs rank third in both numbers of fragments (NISP) and minimum numbers of individuals, but fifth in terms of usable meat. Red deer were the most important wild species, providing as much as a third of the meat at West Row Fen. Their antlers were also employed in the production of a variety of useful artifacts. Roe deer are much smaller and contributed considerably less meat, and their antlers were of little use in tool manufacture.

At Grimes Graves (Fig. 1), in neighboring Norfolk County, the Middle Bronze Age deposits are dominated by cattle, followed closely by caprines, with pigs far behind in third position (Legge, 1992:16–17). However, the ratio of caprines to pigs varies from one region to the next. The Late Bronze Age deposits of Runnymede (Done, 1991) produced slightly more pig than caprine bones, suggesting that fewer forests had been cleared in this area during the Bronze Age. A small collection of bones from Mill Pot Cave, Wetton, Staffordshire, associated with Bronze Age pottery, yielded 76% *Ovis/Capra*, 14% *Bos taurus*, 4% *Sus scrofa*, and 4% *Equus caballus*, based on the minimum numbers of individuals (Ryder et al., 1971).

Most of the Iron Age sites from which there are large faunal assemblages contain predominantly sheep, but these are in downlands that are poorly watered and unsuitable for cattle. There are several Iron Age sites, such as Woodyates, Woodcuts, Longbridge Deverill (phase A), Grimthorpe Hill Fort, and Catcote, where cattle outnumber sheep (Ryder, 1983:79).

West Row Fen, with its three known house structures and large midden, is an important site because Bronze Age settlements of respectable size are rare in Britain, as they are on the continent. The economy of the village, reconstructed from the mammalian remains, implies the degree to which the villagers were sedentary. The possible use of cattle for plowing as well as pulling carts would imply the importance of agriculture relative to herding at West Row Fen. Although pigs rank third in frequency among livestock, their numbers still indicate that the community as a whole was not nomadic (Towne and Wentworth, 1950:69), although shepherds may have left the village seasonally with the caprine herds. The presence of swine suggests that some forests were present, but the greater number of sheep indicates considerable clearing of forests for pasture. Sheep outnumber goats in the fens at this time because of the cool, moist climate of the region and the flat terrain. Red and roe deer are primarily forest dwellers, but their small numbers support the data from sheep that much of the area was cleared for agriculture and grazing. That dogs were eaten is demonstrated by the number of butcher marks on their bones and the treatment of their remains.

ACKNOWLEDGMENTS

I am grateful to the director of the West Row Fen excavations, Edward Martin, of the Suffolk Archaeological Unit, and Sebastian Payne, of English Heritage, for making this research possible. English Heritage funded the research that enabled this report to be written. Edward Martin furnished the map and data in Fig. 2 and 3. Melinda Zeder kindly provided information for distinguishing between sheep and goats. All of the faunal material and bone artifacts from West Row Fen, Mildenhall 165, are the property of English Heritage, Fortress House, 23 Savile Row, London, United Kingdom W1X 2HE.

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TEPHRODYTES BRASSICARVALIS, NEW GENUS AND SPECIES
(ANURA: PELODYTIDAE), FROM THE ARIKAREEAN CABBAGE
PATCH BEDS OF MONTANA, USA, AND
PELODYTID-PELOBATID RELATIONSHIPS

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ABSTRACT

Tephrodytes brassicarvalis, n. gen. and sp., is based on the remains of a nearly complete skeleton, several partial skeletons, and some isolated bones from the Arikareean Cabbage Patch beds of western Montana, USA. It possesses the hallmark pelodytid character of a fused tibiale and fibulare and differs from other known pelodytids in the following unique combination of characters: 1) frontoparietal fontanelle concealed, 2) posterior tip of frontoparietal present, 3) otic plate of squamosal present, 4) otic ramus of squamosal reduced, 5) vertebral neural arches elongate, 6) sacral diapophyses widely expanded, and 7) anterior lamina of scapula absent.

Because the new anuran shares similarities with both pelodytids and pelobatids, and because the pelodytids have been included in the Pelobatidae, a cladistic analysis was undertaken to examine pelodytid-pelobatid relationships. This analysis also examines pelobatoid relationships. Results of this study reveal the following hypotheses of relationships. The Pelobatidae and Pelodytidae are best considered as separate families. *Miopelodytes*, *Pelodytes*, and *Tephrodytes*, whose relationships are unresolved, are members of the Pelodytidae. Similarities between *Tephrodytes* and some of the pelobatids are the result of convergence. Within the Pelobatinae *Eopelobates*, *Macropelobates*, and *Pelobates* form one clade, in which *Eopelobates* and *Pelobates* are sister taxa, and *Scaphiopus* and *Spea* form another. The *Eopelobatinae* is synonymous with the *Pelobatinae*. *Leptobrachium*, chosen as a representative taxon for the *Megophryinae*, is the sister taxon to the *Pelobatinae*.

INTRODUCTION

The Cabbage Patch beds, exposed in the Blackfoot, Flint Creek, Deer Lodge, and Divide intermontane basins of western Montana (Fig. 1), have yielded a diverse fauna that includes mammals, birds, reptiles, amphibians, and fish (Rasmussen, 1989). This study reports a new anuran genus and species, *Tephrodytes brassicarvalis*, in the family Pelodytidae, from these beds. The new taxon is based on a nearly complete skeleton, two partial skeletons, and isolated bones, all of which are well-preserved. They were collected by Donald Rasmussen from localities that he discovered in the Flint Creek Basin in Granite and Powell counties. These specimens and isolated bones are referred to a single species because comparison of them with the holotype, and each other, reveals no significant differences in their morphology. Other taxa of frogs also have been collected by Rasmussen from the Cabbage Patch beds, and these are under study by the author.

The Cabbage Patch beds are Arikareean, late Oligocene-early Miocene in age. During the Arikareean in western Montana a large basin, the Clark Fork Basin, was being filled predominantly with fluvial and lacustrine fine-grained, tuffaceous sediments (Rasmussen, 1989). Rasmussen (1977) suggested that the ash component in these sediments blew in from the west, possibly originating in the Cascades or the Columbia Plateau area, and was deposited in the uplands. From

Submitted 20 April 1993.



Fig. 1.—Map of western Montana showing the location of basins in which the Cabbage Patch beds are exposed (modified from Fields et al., 1985). The basin names are: 1) Blackfoot, 2) Flint Creek, 3) Deer Lodge, and 4) Divide. The pelodytid fossils came from the Flint Creek Basin.

there, Rasmussen (1977) further speculated, the ash was washed into the depositional basins, of which the Clark Fork was one, and was extensively reworked before final deposition. Only remnants of this formerly widespread unit exist today in the Flint Creek and adjacent basins (Rasmussen, 1989). The depositional environments of the three localities the fossils came from were determined to be fluvial overbank for localities KU-MT-12 and KU-MT-25, and lacustrine for locality KU-MT-8 (Rasmussen, 1977). The holotype came from KU-MT-25.

The Pelodytidae was named by Bonaparte in 1850 (Frost, 1985), although Cope (1866) is often given credit for naming the family. Boulenger (1897) included the pelodytids in the Pelobatidae, and since then the pelodytids have been ranked either as a separate family (Taylor, 1941; Lynch, 1973; Duellman, 1975; Sanchiz, 1978; Laurent, 1979; Dubois, 1983; Frost, 1985; Cannatella, 1985; Duellman and Trueb, 1986) or incorporated with the Pelobatidae (Noble, 1924, 1931; Griffiths, 1963; Kluge and Farris, 1969; Vergnaud-Grazzini, 1970; Špinar, 1972; Savage, 1973). More recent classifications consider the pelodytids a separate family (Lynch, 1973; Duellman, 1975; Laurent, 1979; Dubois, 1983; Frost, 1985; Cannatella,

1985; Duellman and Trueb, 1986; Ford and Cannatella, 1993). Because *Tephrodytes* possesses several features (sculpturing on the dermal skull bones, presence of posterior tip of the frontoparietal, frontoparietals cover frontoparietal fontanelle, squamosal articulates with maxilla, and presence of elongate vertebral neural arches) that also occur in some pelobatids, but were previously unreported for the pelodytids, an examination of the pelodytid–pelobatid relationship is warranted. Thus a cladistic analysis was undertaken to see if the new information from *Tephrodytes* helps to resolve whether the pelodytids should be placed in the Pelobatidae or in their own family. This analysis also addresses pelobatoid relationships which were unresolved in the cladistic analysis of anurans undertaken by Ford and Cannatella (1993).

The holarctic family Pelodytidae is not very diverse. Two extant species of *Pelodytes*, *P. punctatus* and *P. caucasicus*, occur in southwestern Europe and the Caucasus region of southeastern Asia, respectively (Frost, 1985). The occurrence of *Pelodytes* in the middle Pleistocene of France was recorded by Rage (1969) and he questionably referred some of the fossils to *P. punctatus* (Rage, 1972). *Pelodytes arevacus* and specimens attributed to *Pelodytes* are known from the middle Miocene of Spain (Sanchiz, 1978). *Miopelodytes* was the only pelodytid previously known from North America, and it is based on a single specimen from the middle Miocene Elko shales near Elko, Nevada (Taylor, 1941). Additional material, including tadpoles, has been collected from this locality and are being described by Dr. Ted Cavender (personal communication). *Propelodytes wagneri*, from the middle Eocene of Messel, Germany, was considered to be a pelodytid by Weitzel (1938). However, both Hecht (1963) and Sanchiz (1978) cast doubt on this assignment, and Wuttke (1988) has referred to these specimens as *Eopelobates wagneri*.

According to the most recent classification that includes fossil taxa (Duellman and Trueb, 1986) the family Pelobatidae includes 13 genera in three subfamilies. Seven of these are in the Megophryinae, which has no fossil record, and they occur in southeastern Asia and from the Indo-Australian Archipelago to the Philippine Islands (Duellman and Trueb, 1986).

The Eopelobatinae (Špinar, 1972) originally included only *Eopelobates*, which has a holarctic distribution and ranges from the early Eocene to the Pliocene. Nessov (1981) later added *Aralobatrachus* and *Kizylkuma*, which are based on isolated elements from the late Cretaceous of Uzbekistan, but these taxa have since been reassigned to the Discoglossidae (Roček and Nessov, 1993). Studies of the development of the frontoparietal by Roček (1981, 1988) have revealed that the frontoparietal in *Eopelobates bayeri* consists of three ossifications instead of two. The presence of the median ossification has been inferred for *E. anthracinus*, the genotype, and this character is included in the revised diagnosis for the genus (Špinar and Roček, 1984). Because the frontoparietal is apparently paired in the North American *Eopelobates grandis* and *E. guthriei*, Roček (1981) suggested that they are probably more closely related to *Scaphiopus* than to *Eopelobates*. I agree with his suggestion concerning *E. guthriei*. However, *E. grandis* possesses several features that do not support a close relationship with *Scaphiopus*. Both specimens are currently under study by the author. Kuhn (1941) described seven genera containing eight species that Estes (1970) later synonymized as *Eopelobates hinschei*. However, Roček (1981) questioned the taxonomic placement of these taxa, in part because the frontoparietal is apparently paired. Hereafter, discussion concerning *Eopelobates* will be limited to the well-described *E. anthracinus* and *E. bayeri*.

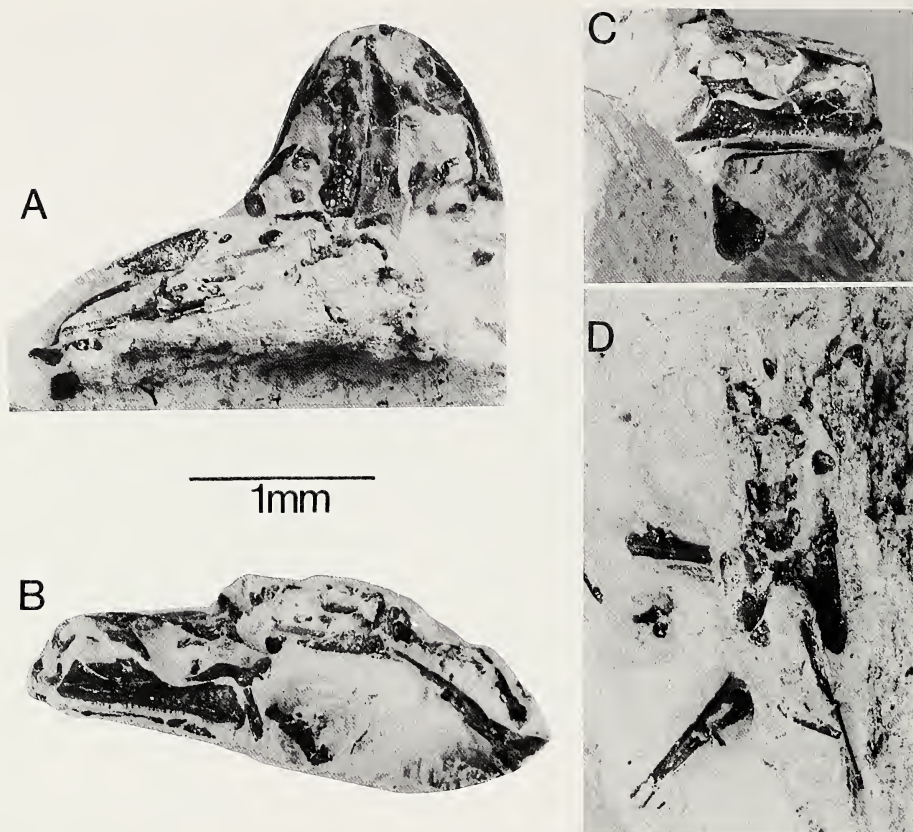


Fig. 2.—Photographs of the holotype of *Tephrodytes brassicarvalis*, KU 19928. A, dorsal view; B, left lateral view; C, right lateral view; and D, counterpart.

The fossorial Pelobatinae consists of the middle Oligocene *Macropelobates* from Mongolia, the extant *Pelobates* from Europe, western Asia, and North Africa, and the extant *Scaphiopus* from southern Canada to southern Mexico. The earliest record for *Pelobates* is the late Eocene of Belgium (Böhme et al., 1982) and that for *Scaphiopus* is the middle Oligocene of North America (Estes, 1970). If *E. guthriei* is indeed a species of *Scaphiopus*, then the record can be extended back to the early Eocene.

ABBREVIATIONS

Anatomical.—Al, anterior lamina of scapula; As, angulosplenic; At, anterior tubercle of scapula; C, columella; Cl, clavicle; D, dentary; Ex, exoccipital–prootic complex; F, femur; Fp, frontoparietal; H, humerus; Il, ilium; Is, ischium; M, metatarsals; Mx, maxilla; N, nasal; Op, otic plate of squamosal; Or, otic ramus of squamosal; Pal, palatine process of maxilla; Pm, premaxilla; Po, postorbital process of frontoparietal; Pp, posterior process of maxilla; Qj, quadratojugal; R, radio-ulna; S, sacrum; Sc, scapula; Sp, sphenethmoid; Sq, squamosal; Tf, tibiofibula; tTF, fused tibiale and fibulare; U, urostyle; V, vertebra; Zp, zygomatic process of maxilla.

Institutional.—AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; KU, University of Kansas, Museum of Natural History; UNSM, University of Nebraska State Museum; and USNM, United States National Museum.

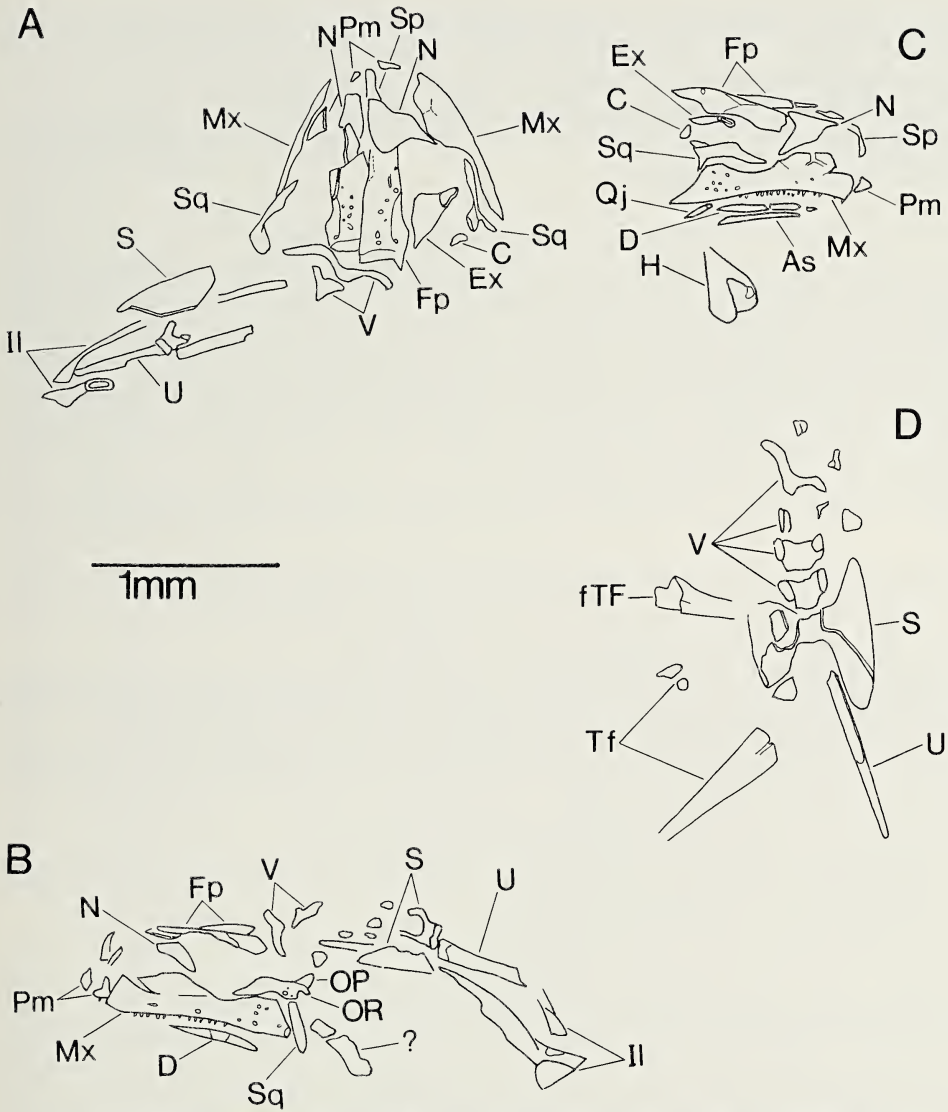


Fig. 3.—*Tephrodytes brassicarvalis*, KU 19928. Line drawings of same views as in Fig. 2.

SYSTEMATIC PALEONTOLOGY

Class Amphibia

Order Anura

Family Pelodytidae

Tephrodytes, new genus

Type Species.—*Tephrodytes brassicarvalis*, new species.

Diagnosis.—*Tephrodytes* differs from all other pelodytids by having frontoparietals that meet medially to conceal the frontoparietal fontanelle. It differs from *Pelodytes* in the following unique combination of characters that are not known for *Miopelodytes*: 1) posterior tip of frontoparietal present, 2) otic plate of squa-

mosal present, 3) presacral vertebral neural arches elongate, and 4) anterior lamina of scapula absent. It is distinguished from *Miopelodytes* by possession of reduced otic ramus of squamosal and expanded sacral diapophyses.

Etymology.—From the Greek *tephra*, ashes, and *dytes*, diver, enterer; in reference to the tuffaceous sediments from which this frog was recovered, and in which it may have estivated.

Tephrodytes brassicarvalis, new species

Holotype.—KU 19928 (Fig. 2, 3): partially complete, loosely articulated skeleton. The skull includes both frontoparietals, nasals, premaxillae, maxillae, squamosals, right ?quadratojugal, right exoccipital–prootic complex, right ?columella, right pterygoid, and both dentaries and angulosplenials. The postcranial skeleton is preserved in part and counterpart and includes: fourth through eighth vertebrae, sacral vertebra, urostyle, right humerus, right radio-ulna, both ilia, right tibiofibula, and right fused tibialae and fibulae.

Type Locality and Horizon.—KU-MT-25, Cabbage Patch #10; Flint Creek Basin, Powell County, Montana. Lower Cabbage Patch beds, Arikareean.

Referred Specimens.—From the type locality: KU 19221, partial left frontoparietal, left exoccipital–prootic complex, and vertebral column; KU 23489, right scapula and clavicle, sacral vertebra, urostyle, ilia, and hindlimbs; KU 18191, right maxilla; KU 19940, left maxilla; KU 18195, right ilium; KU 19917, left ilium; KU 19918, right ilium; KU 19919, right ilium.

From locality KU-MT-12, Cabbage Patch #4, Flint Creek Basin, Granite County, Montana, Middle Cabbage Patch beds, Arikareean: KU 18266, proximal half of right humerus; KU 18270, proximal end of fused tibialae and fibulae; KU 18273, proximal end of fused tibialae and fibulae.

From locality KU-MT-8, Pikes Peak #1, Flint Creek Basin, Powell County, Montana, Upper Cabbage Patch beds, Arikareean: KU 20654, sacrum; KU 20659, complete right humerus and proximal end of left humerus from different individuals.

Diagnosis.—As for genus (currently monotypic).

Etymology.—From the Latin *brassica*, cabbage, and *arvalis*, of a cultivated field, in reference to the Cabbage Patch beds.

Description

The holotype (Fig. 2, 3) is a three-dimensionally preserved, nearly complete skeleton in which the cranial bones are very closely associated. Its length, from tip of snout to distal end of urostyle, is approximately 4.0 cm. That this specimen had achieved adulthood before death is suggested by the well-ossified bones of the skull and postcranial skeleton. Measurements of complete bones appear in Table 1. The following description is based on the holotype unless otherwise stated.

Skull.—Both halves of the subrectangular frontoparietals are preserved in KU 19928 (Fig. 2A, 3A). The right half is slightly crushed along a small portion of the medial edge and its anteriormost end is covered by the right nasal. In the left frontoparietal the anterior half of the lateral edge is broken away, the postero-medial end lies underneath the posterior end of the right frontoparietal, and the posterior tip is covered by matrix and the left transverse process of the third vertebra.

The frontoparietal is widest near the posterior end (Fig. 2A, 3A, 4A). From the posterior end it narrows to the midpoint of its length where it flares slightly in a lateral direction to form the postorbital process (Fig. 4A). From there to the

Table 1.—Measurements for all complete bones of *Tephrodytes brassicarvalis*. The holotype is KU 19928.

	KU 18191	KU 19221	KU 19917	KU 19918	KU 19928	KU 20654	KU 20659	KU 23489
Frontoparietal length					7.3			
Frontoparietal width					2.0			
Nasal length					3.1			
Nasal width					4.5			
Maxilla length	12.5				10.4			
8th vertebra length		2.4			1.9			
Sacral diapophyses length					7.8	9.9		5.0
Sacral diapophyses width					6.8	8.0		
Urostyle length					11.2			
Scapula length								3.5
Humerus length							9.7	
Ilium length			20.7	17.5	18.3			14.0
Femur length								13.1
Tibiofibula length								13.9
Tibiale-fibulare length								6.8

anterior end the frontoparietal is slightly narrower (Fig. 3A). The medial edge of the left frontoparietal, where exposed, is straight. In Fig. 2 and 3, however, crushing along the medial edge of the right frontoparietal causes it to appear as though it is tapering. The posterolateral corner of the frontoparietal is drawn out to a point, the posterior tip (=processus paroccipitalis of Roček, 1981), which is oriented posteriorly. I prefer to use Estes' (1970) term posterior tip instead of the processus paroccipitalis of Roček (1981) to avoid confusing this process with the paroccipital process of the occiput.

Light sculpturing in the form of pits and grooves occurs on the relatively flat dorsal surfaces of the frontoparietals. The sculpturing is most pronounced on the posterolateral corner and is absent along the medial edge. In KU 19221 (Fig. 4A), a larger individual than the holotype, the posterior half of one frontoparietal is preserved. Sculpturing covers most of its dorsal surface, and the pits and grooves are larger.

Unlike other pelodytids the frontoparietal fontanelle was not exposed in *Tephrodytes*. In some anurans that have an exposed fontanelle, such as *Spea*, the frontoparietals are sutured together only at the posterior end. From there anteriorly the two halves are free, which allows exposure of the fontanelle. In *Pelodytes*, which also has an exposed frontoparietal fontanelle, even the posterior ends of the frontoparietals are not in contact. Concerning *Tephrodytes* the preserved portion of frontoparietal in KU 19221 has several small indentations along the medial edge which are interpreted here as a zigzagging suture scar (Fig. 4A). This provides evidence that the posterior halves of the frontoparietals were sutured together. In the holotype the medial edge of the right frontoparietal does not taper, indicating that the two halves would have been in contact, thus covering the fontanelle.

Nasal bones are preserved only in the holotype. The right is undistorted (Fig. 2A, 3A) but the left is incomplete and its posteromedial corner is covered by the anterior end of the left frontoparietal. The area where the two nasals meet medially

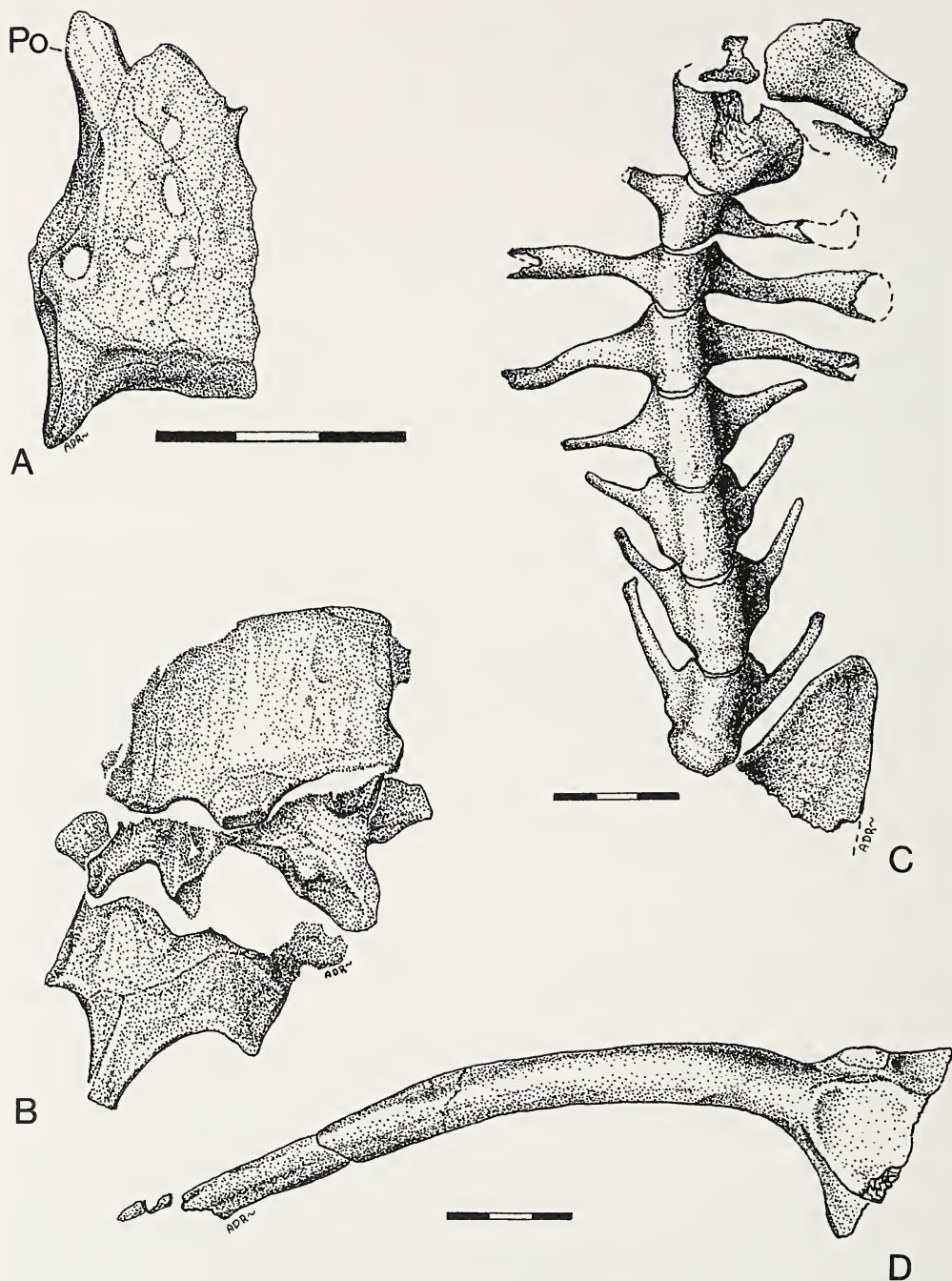


Fig. 4.—*Tephrodytes brassicarvalis*. A, posterior half of frontoparietal, KU 19921; B, presacrals 1–3, KU 19921; C, vertebral column and part of sacral diapophysis, KU 19921; and D, right ilium, KU 19917. Scale in mm, in which A and B are drawn to same scale.

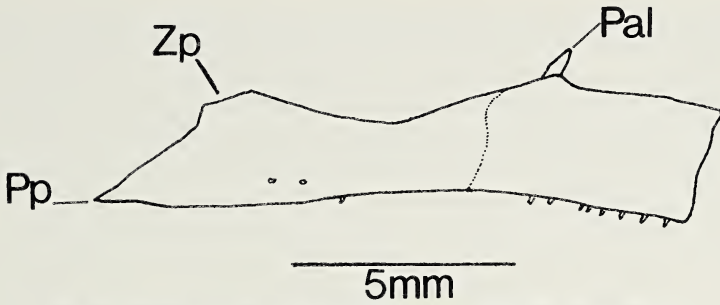


Fig. 5.—Right maxilla of *Tephrodytes brassicarvalis*, KU 18191.

is relatively long. The width of the right nasal is greater than its length (Table 1). Its anterior process is a small nubbin, and the concave anterolateral margin forms the posteromedial border of the external narial opening. Laterally, the nasal is drawn into a maxillary process which is directed posterolaterally (Fig. 2C, 3C). There is no sculpturing on the dorsal surface of the nasals.

The right and left premaxillae, which bear teeth, are preserved in the holotype (Fig. 2B, C; 3B, C). Here, the lateral ends of both premaxillae are overlain by the medial ends of the maxillae. The medial end of the left premaxilla is covered by the medial end of the right premaxilla. This telescoping causes the snout to appear narrower than it actually is. The alary process is elongate in the left premaxilla and incomplete in the right. Sculpturing is light and occurs as tiny pits but does not extend onto the alary process.

Both maxillae are preserved in the holotype (Fig. 2A, B, C; 3A, B, C). Two isolated maxillae (KU 18191, Fig. 5; and KU 19940) have also been recovered. In the holotype the pars facialis of the maxilla is slightly crushed at the anterior end where it reaches its greatest height. The pars facialis pinches in at the level of the orbit and increases in height at the posterior end to form the zygomatic process. In KU 18191 the dorsal surface of the zygomatic process is exposed and bears a suture scar, which provides evidence that the zygomatic ramus of the squamosal articulated with it. The posteroventral end of the maxilla is drawn into a point, the posterior process, which extends posteriorly beyond the level of the zygomatic process. Small teeth are present on the pars dentalis for about $\frac{3}{4}$ the length of the bone from its anterior end. In the holotype the tip of a tooth that was prepared appears to be fang-like and recurved medially. In medial aspect, in KU 19940, the palatine process arises off the medial face of the pars facialis just dorsal to the pars palatina. In this specimen the tip of the palatine process is broken off at the level of the dorsal edge of the pars facialis. In KU 18191, exposed in lateral view, the tip of the palatine process extends beyond the dorsal edge of the pars facialis. It seems likely that the palatine process was long enough to reach, and articulate with, the lateral wing of the sphenethmoid, as in other pelobatoids. Sculpturing in the holotype is light and occurs as pits and grooves which are larger at the posterior ends of the maxillae. In KU 19940, the largest maxilla, only a few pits are present on the posterior end.

In the holotype there is a sliver of bone located adjacent to the posteroventral edge of the right maxilla. Based on its position and size it is believed to be the quadratojugal. Even if this bone is not the quadratojugal its presence in *Tephrod-*

yes is suggested by the presence of a posterior process of the maxilla. Estes (1970) has implied that anurans possessing a posterior process also have a quadratojugal. To test Estes' theory I examined the skull of all anuran taxa in the CM amphibian osteology collection. With the exception of *Scaphiopus* and *Spea* all possessed a quadratojugal and the maxilla bore a well-developed posterior process. *Scaphiopus* and *Spea* were the only taxa that lacked a quadratojugal, and the posterior process of the maxilla was reduced or absent in these taxa.

Both squamosals are preserved in the holotype. The left squamosal is complete (Fig. 2A, B; 3A, B) and the right is missing the otic plate (Fig. 2A, C; 3A, C). The squamosals are pushed anteriorly out of position so that the ventral ramus of each is adjacent to the posterior end of the maxilla, causing the skull to appear shorter than it actually is. The zygomatic ramus of the squamosal is relatively thin and long, reaching its greatest thickness near the midpoint of its length. The otic ramus, in lateral aspect, is reduced to a nubbin. Projecting medially from the otic ramus is the otic plate which would overlap the crista parotica of the exoccipital-prootic complex, if the bones of the skull were articulated. The medial end of the otic plate is rounded. Sculpturing, consisting of a few large pits and some tiny pits, is mostly confined to the area where the three rami meet. A few small pits occur on the zygomatic ramus as well.

Only the right exoccipital-prootic complex is preserved in the holotype (Fig. 2A, 3A). Its medial end is pushed under the right frontoparietal and the lateral end is missing. There is a left exoccipital-prootic complex in KU 19221 in which the left frontoparietal covers its dorsal surface and the left parasphenoid alae covers its ventral surface. In this specimen the medial wall of the auditory capsule is exposed revealing the anterior and posterior acoustic foramina and the superior and inferior perilymphatic foramina. The presence of a dorsal endolymphatic foramen cannot be determined because of damage in the area where it would occur. The prootic foramen is not completely surrounded by bone.

A small, T-shaped bone lies ventral to the right exoccipital-prootic complex and medial to the posterior end of the right squamosal in the holotype. Based on its shape and position it is believed to be the medial end of the right columella. Note that only the footplate of the columella is visible in Fig. 3A and C. A small bone was found ventral to the columella and has been removed. This element is domed shaped, with a smooth dorsal surface and a rough ventral surface. Possibly it is a calcified operculum. It is equally possible that it is merely a fragment of weathered bone. The occurrence of a calcified operculum in a fossil frog is not unprecedented, as Kluge (1966) documented the presence of one in the lower Miocene *Scaphiopus neuter*. Unfortunately, I have been unable to compare the operculum of *S. neuter* with the possible operculum of *Tephrodytes*.

Preparation of the palatal region is hindered by the presence of the humerus, radio-ulna, and several unidentified bones underneath the skull. The right pterygoid, exposed in ventral view, bears an elongate anterior ramus, the anterior end of which lies between the lower and upper jaws. Although the exact length of the anterior ramus cannot be determined, it is unquestionably greater than twice the length of the medial ramus. The short medial ramus has a blunt medial end. The triangular posterior ramus is the shortest of the three rami. A portion of the left vomer is exposed in the holotype. Although several tooth sockets of the vomer are visible, no other details can be discerned.

Both lower jaws have been pushed dorsally inside the mouth of *Tephrodytes*. Not much of either dentary could be exposed by preparation because the maxillary

teeth overlap them (Fig. 2B, C; 3B, C). Only part of the angulosplenic (Fig. 2C, 3C) could be prepared without causing damage to the rest of the skull. Neither bone exhibits any noteworthy features.

Postcranial Skeleton.—The vertebral column is preserved as part and counterpart in the holotype (Fig. 2D, 3D). Presacrals four through eight and the sacrum are exposed, but there is considerable damage. In KU 19921 the eight presacrals and part of the left sacral diapophysis are exposed in ventral view (Fig. 4C), the atlas and first three presacrals are exposed in dorsal view (Fig. 4B), and the bone is well-preserved in all. The following description is based on KU 19921.

The eight presacral vertebrae have imbricate neural arches, as indicated by the elongate neural spine of the third presacral, the only one completely preserved and exposed (Fig. 4B). That the vertebrae are procoelous is best demonstrated in the seventh and eighth presacral (Fig. 4C). The atlantal cotyles of the atlas are closely juxtaposed. The dorsal surface of the atlantal neural arch is smooth. Its posterior end is drawn out to form the neural spine, the posterior end of which is broken off. Transverse processes of the second through fourth vertebrae are elongate and directed laterally, except for the fourth which is directed slightly posteriorly. The transverse processes of the fifth through eighth vertebrae are thinner and shorter. Those of the fifth are directed laterally, the sixth moderately anteriorly, and the seventh and eighth strongly anteriorly. Free ribs are not preserved and are presumably absent.

The sacral vertebra is preserved in the holotype (Fig. 2D, 3D), KU 23489 (Fig. 6), and KU 20654 (isolated sacrum). The diapophyses are widely expanded and their length is greater than their width. In the holotype length was determined from the right diapophysis of the counterpart. The width was determined by doubling the distance from the lateral edge of the left diapophysis to the middle of the centrum. In the holotype the length of the sacral diapophyses is roughly equivalent to the length of the last four presacrals. The length of four presacrals was determined by measuring the length of the eighth presacral, which has been exposed in dorsal view by preparation, and multiplied by four. Variation in the shape of the sacral condyle occurs. It is monocondylar in KU 23489, forming a dorsoventrally compressed oval and distinctly bicondylar in KU 20654. In the holotype it is neither distinctly monocondylar nor bicondylar but instead forms a flattened oval that is slightly pinched in the middle.

The urostyle is preserved as part and counterpart in the holotype (Fig. 2A, D; 3A, D), and in KU 23489 (Fig. 6) the anterior half of the urostyle is exposed. In the holotype it is at least as long as the last five presacral vertebrae. Transverse processes on the urostyle are not apparent in either example.

A right scapula and clavicle, exposed in KU 23489 (Fig. 6, 7B), are the only preserved bones of the shoulder girdle. The short, stocky scapula bears both the pars acromialis and glenoidalis on the ventral end and they are narrowly separated at their distal ends. Arising from the anterior edge of the scapula near the pars acromialis is the anterior tubercle. An embayment lies between it and the pars acromialis. The anterior tubercle also occurs in *Pelodytes*, and in that taxon the clavicle reaches the ventral edge of the anterior tubercle, and thus overlaps the scapula anteriorly. Because the ventral end of the scapula of *Tephrodytes* is very similar in shape to that of *Pelodytes*, it is inferred that the scapula is anteriorly overlain by the clavicle in *Tephrodytes*. In *Tephrodytes* the bone along the anterior edge of the scapula is somewhat thick and rounded, and the margin is concave. Thus, there is no anterior lamina.

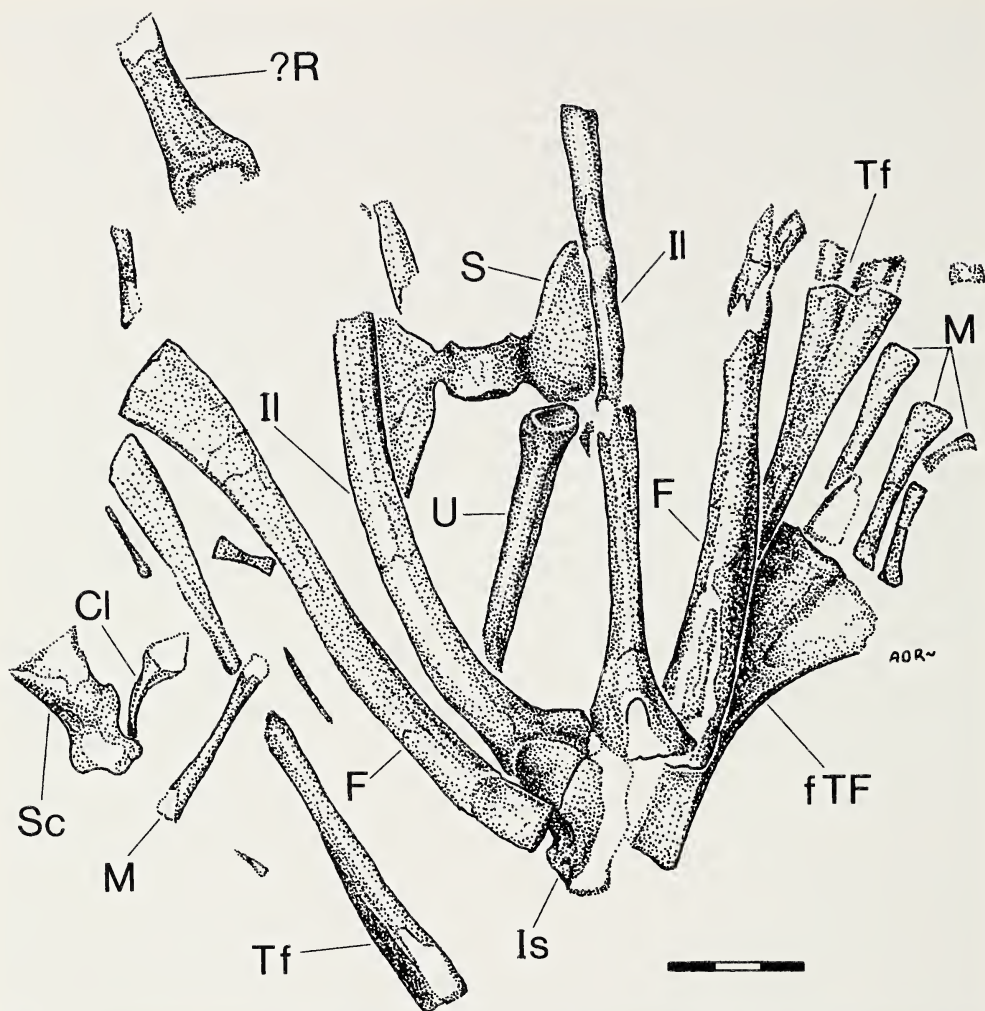


Fig. 6.—Postcranial skeleton of *Tephrodytes brassicarvalis* as preserved in KU 23489. Scale in mm.

The clavicle is oriented almost vertically in the matrix (Fig. 6). The process on the lateral end that articulates with the scapula is broken off and the medial end lies under the scapula. Enough of the clavicle is preserved to show that it is bowed, which suggests that the shoulder girdle of *Tephrodytes* is arciferal. The preserved portion of the clavicle is roughly the same length as that of the scapula. Thus, if the clavicle was complete it would be longer than the scapula.

The right humerus (Fig. 2C, 3C) and radio-ulna are preserved in the holotype in articulation. Here the humerus is exposed in dorsal and lateral views and the proximal third of this bone is missing. Also, there are three isolated humeri (KU 18266 and 20659, two humeri). The following description is based on KU 20659, a complete humerus. The shaft is straight and bears the crista ventralis on its proximal half. The triangular fossa is not very deep. Well-developed medial and lateral epicondyles bound the round humeral ball. The medial epicondyle pro-

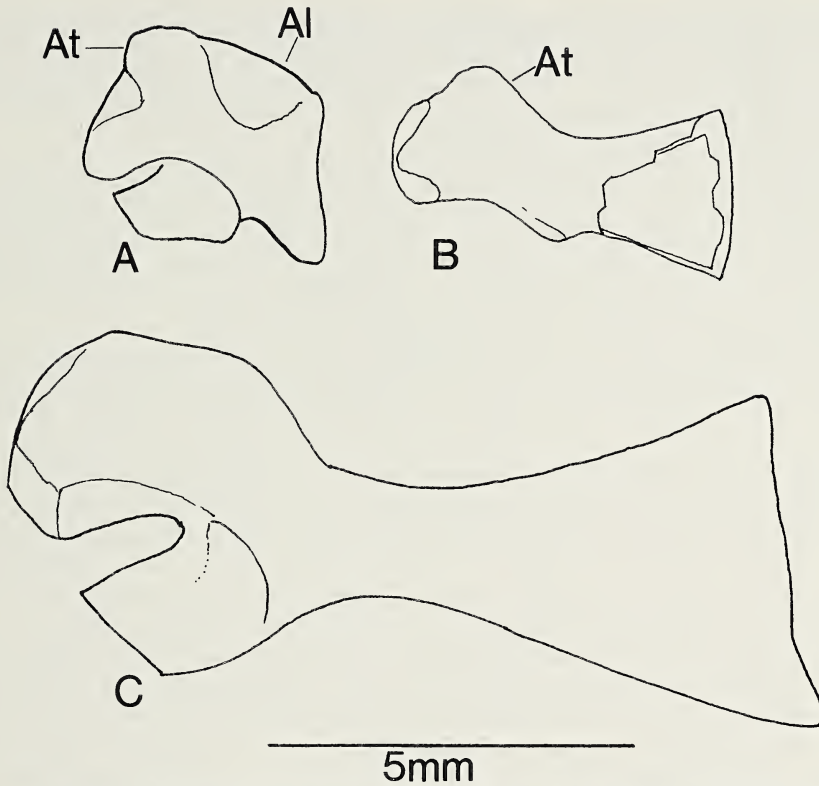


Fig. 7.—Comparison of scapula from specimens of similar size. A, *Pelodytes punctatus*, CM 54754; B, *Tephrodrytes brassicarvalis*, KU 23489; C, *Scaphiopus holbrooki*, CM 92261.

trudes medially, is triangular in medial aspect, and is joined to the shaft by a thin crest. The smaller lateral epicondyle is crest-like. In lateral view a groove, the surface of which is covered with finished bone, lies between the roughened bone of the lateral epicondyle and the ball. The triangular olecranon scar is medially situated.

The radio-ulna is exposed in lateral view, and the anterior half of the bone is also exposed in dorsal view. The posterior end is poorly preserved, hindering its preparation. The olecranon process is rounded. A sulcus is not visible on the anterior half of the shaft. Also, in KU 23489 there is a bone that is possibly a radio-ulna (Fig. 6).

Both ilia are preserved in the holotype. The left is complete whereas the right is missing most of its shaft. There are several isolated ilia; the best preserved is KU 19917 (Fig. 4D). In that specimen, the shaft, which lacks crests, is bowed ventrally and has an oval cross section. The dorsal acetabular expansion bears an oval, dorsolaterally-projecting dorsal protuberance which has roughened, unfinished bone on its surface. This protuberance is larger in KU 19917 than in the holotype, which is a smaller individual. A groove runs from the shaft to the dorsal acetabular expansion. The ventral acetabular expansion and the dorsal acetabular expansion are subequal in length. The acetabulum is large, roughly bell-shaped, and somewhat deep. Its dorsal border projects slightly from the lateral surface of

the dorsal acetabular expansion whereas the ventral border projects strongly from the lateral surface of the ventral acetabular expansion. The dorsal ends of both ischia are preserved in KU 23489 (Fig. 6), in which they appear to be medially fused. The ischia do not extend greatly posteriorly as occurs in *Eopelobates* and *Megophrys* (Zweifel, 1956; Estes, 1970).

Both femora and tibiofibulae are preserved in KU 23489 (Fig. 6) and partial tibiofibulae occur in the holotype. The femur is slightly S-shaped, and the distal end is wider than the proximal end. Presence of a femoral crest cannot be determined because of the orientation of the femora in the matrix. In KU 23489 the tibiofibula is slightly longer than the femur (Table 1). The longitudinal sulcus of the tibiofibula is restricted to the proximal and distal ends.

Complete fusion of the tibiale and fibulare occurs in *Tephrodytes*. The left fused tibiale and fibulare is preserved in the holotype where it lies underneath the sacrum (Fig. 2D, 3D). In KU 23489 a left fused tibiale and fibulare is partly overlain by other bones (Fig. 6). Two isolated fused tibiale and fibulare (KU 18270 and 18273, Fig. 8) were recovered as well. In the former two examples the longitudinal sulcus is restricted to the proximal and distal ends. In the latter two examples, which are considerably smaller and missing their extreme distal ends, the longitudinal sulcus extends most of the length of the bone. The latter two bones are probably from juveniles. In all examples, the fused tibiale and fibulare have an hourglass shape and a small foramen is located near the midpoint of the shaft.

Only a few metatarsals and phalanges are preserved in KU 23489 and the holotype making it impossible to determine the phalangeal formula. Metatarsals 1-4 are preserved very close to the distal end of the left fused tibiale and fibulare (Fig. 6). A small phalanx is associated with metatarsal 1. None of the distal tarsal bones are preserved; possibly they were cartilaginous. A prehallux modified as a spade has not been found and presumably was absent, as in *Pelodytes*.

Family Assignment

Tephrodytes brassicarvalis possesses a fused tibiale and fibulare, which occurs only in the frog families Pelodytidae and Centrolenidae. Of the numerous characters that distinguish the pelodytids from the centrolenids (Duellman and Trueb, 1986) three are preserved in *Tephrodytes*, and are: the atlantal cotyles are closely juxtaposed, the vertebral neural arches are imbricate, and the sacral diapophyses are widely expanded. *Tephrodytes* possesses no characters that occur in the centrolenids but not in the pelodytids, thereby making its affinity with the pelodytids certain. Those characters that would indicate centrolenid affinities are: nonimbricate neural arches, dilated sacral diapophyses, and scapula not overlain anteriorly by clavicle.

During the course of this study I became aware of some inconsistencies in several of the characters used in different definitions of the Pelodytidae. Taylor (1941), Lynch (1973), and Duellman and Trueb (1986) all included in their definitions the fusion of presacral vertebrae I and II. None of the eight specimens of *Pelodytes punctatus* that I examined had fused presacral vertebrae. They were also free in the *P. punctatus* specimens examined by Cannatella (1985). Sanchiz (1978), however, observed the free state in *Pelodytes arevacus*, *P. caucasicus*, and both the free and fused states in *Pelodytes punctatus*. He concluded that in *P. punctatus* the free state occurred in both subadults and adults. Zweifel (1956), apparently following Taylor (1941), stated that they are fused in *Pelodytes*, although neither author mentioned which species were examined. In *Miopelodytes*

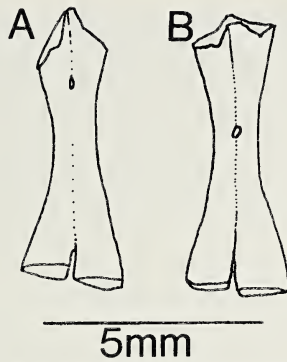


Fig. 8.—Fused tibiale and fibulare of *Tephrodytes brassicarvalis*. A, KU 18273; B, KU 18270.

Taylor observed that the first two presacrals are fused. However, I found this impossible to determine in *Miopelodytes* because of bone damage. Thus, fusion of presacrals I and II is not diagnostic of the family and appears to be variable in *Pelodytes*.

In his definition of the Pelodytidae, Lynch (1973) reported that the articulation between the sacrum and the urostyle is monocondylar, whereas in their definition of the family, Duellman and Trueb (1986) stated that it is bicondylar. Furthermore, Boulenger (1896), Taylor (1941), and Rage (1974) observed that the articulation is bicondylar, and Cannatella (1985) reported it as monocondylar. Zweifel (1956) suggested that the type of articulation varies intraspecifically. Sanchiz (1978) contested Zweifel's (1956) conclusion because he observed that the sacral condyle of *Pelodytes arevacus* and *P. punctatus* has a unique condition of being intermediate between the monocondylar and bicondylar states. In *Tephrodytes* the form of the sacral condyle varies, being either monocondylar, bicondylar, or the intermediate condition described by Sanchiz (1978). The type of articulation cannot be determined for *Miopelodytes*. Thus, it appears that the type of articulation between the sacrum and urostyle is a variable feature within the family.

Both Lynch (1973) and Duellman and Trueb (1986) included the presence of transverse processes of the urostyle in their definitions of the Pelodytidae. However, of the eight specimens of *Pelodytes punctatus* that I examined, only one possessed distinct transverse processes on the urostyle. In this specimen, CM 54318F, the process on the right side is well-developed whereas that of the left is a nubbin. The presence or absence of transverse processes does not appear to be the result of variation between the sexes because they were both present and absent in the females examined. Age as the cause of variation can be ruled out because the specimens examined were of similar size. Geographical variation also is not a factor because the specimens were from a single locality. Neither *Miopelodytes* nor *Tephrodytes* bears transverse processes on the urostyle. Thus, the presence of transverse processes of the urostyle varies in *P. punctatus*, has not been reported for either *Miopelodytes* or *Tephrodytes*, and should not be regarded as a diagnostic character of the family.

Evans and Milner (1993) noted that the ilia of *Pelobates* possess a spiral groove at the base of the shaft whereas pelodytids lack this groove. All of the pelodytid and pelobatid specimens that I examined possess this spiral groove, with the exception of *Miopelodytes*. The presence of a spiral groove could not be determined

in *Miopelodytes* because of damage to the ilium. Also, Sanchiz's (1978) illustrations of the ilium of *Pelodytes arevacus* and *P. punctatus* depict a groove. This character is possibly diagnostic of the Pelobatoidea, although I have not surveyed its distribution outside of the primitive anurans.

PELOBATOID RELATIONSHIPS

The monophyly of the Pelobatoidea has been established by Cannatella (1985), and confirmed by Ford and Cannatella (1993). Supporting synapomorphies for this hypothesis of relationship are the presence of an ossified sternum, the presence of a palatine process of the maxilla (Cannatella, 1985; Ford and Cannatella, 1993), and the presence of the adductor longus muscle (Cannatella, 1985). Cannatella (1985) deviated from traditional classifications that include the megophryines in the Pelobatidae by placing the megophryines in their own family, the Megophryidae. Following his taxonomy, the Pelobatoidea thus includes the Megophryidae, Pelobatidae, and Pelodytidae. He concluded, based on a cladistic analysis of primitive anurans, that the pelodytids and pelobatids are more closely related to each other than either is to the megophryids. Fossil taxa were not included in his study. However, Ford and Cannatella (1993), in a cladistic analysis of anurans, determined that the Megophryidae, Pelobatidae, and Pelodytidae form an unresolved trichotomy. The extinct Eopelobatinae were removed from the Pelobatidae by Ford and Cannatella (1993) because these workers questioned the monophyly and relationships of this group. Thus, they considered the Eopelobatinae to be a metataxon, having either uncertain relationships within the Pelobatoidea or comprising a sister group to the Pelobatoidea. This left *Pelobates*, *Scaphiopus*, and *Spea* as the remaining members of the Pelobatidae. The extinct pelobatine *Macropelobates* was not included in their study.

Previous studies have suggested somewhat different hypotheses of relationships. Lynch (1973) proposed that the pelodytids are the sister group of the pelobatids and higher anurans, whereas Sokol (1981) suggested that *Pelodytes* is most closely related to the megophryine and pelobatine pelobatids. Boulenger (1899) hypothesized that *Pelodytes* is more closely related to *Pelobates* than to *Scaphiopus*.

There has been considerable debate concerning the relationship of the extinct *Eopelobates* and *Macropelobates* to other pelobatids. Zweifel (1956) suggested that *Eopelobates* could be a subgenus of the megophryine genus, *Megophrys*. Similarly, Kluge (1966) considered *Eopelobates* to be more closely related to the megophryines than to the pelobatines. Estes (1970) observed that *Eopelobates* is a primitive member of the family that is similar to both the megophryines and the pelobatines. However, the above conclusions were based, in part, on examination of *E. grandis* and *E. guthriei*, which may not be species of *Eopelobates* (Roček, 1981). Derivation of the pelobatines and the megophryines from the eopelobatines was suggested by Špinar (1972). Roček (1981), on the other hand, observed that both *Eopelobates* and *Pelobates* possess a frontoparietal derived from three ossifications, a right and left ossification and a medial ossification situated posterior to them. He homologized the medial ossification with the extrascapular of *Eusthenopteron*. Because *Eopelobates* and *Pelobates* are the only anurans known to share this feature, Roček (1981) concluded that they evolved separately from all other anurans. This hypothesis was rejected on the basis of parsimony by both Cannatella (1985) and Milner (1988), and Milner has further suggested that the medial ossification is merely a synapomorphy defining a clade within the Pelobatidae.

A common ancestor, possibly *Macropelobates* (Noble, 1924), or a form close to *Macropelobates* (Zweifel, 1956; Estes, 1970) has been suggested for *Scaphiopus* and *Pelobates*, although Estes (1970) has cautioned that *Macropelobates* occurred too late in time to be the actual ancestor. Roček (1982) theorized that *Macropelobates* is more closely related to *Scaphiopus* than *Pelobates* based on morphological similarities and paleogeographical grounds. The Turgai Straits, which separated Europe and Asia from the Jurassic to the Eocene, would have prevented dispersal of pelobatines into Europe from an Asian ancestor (Roček, 1982).

Cladistic Analysis

To obtain a better understanding of the interrelationship of the pelobatoids, a cladistic analysis was undertaken. Representative pelobatoids employed in the ensuing character analysis are as follows: *Leptobrachium*, *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, *Spea*, *Miopelodytes*, *Pelodytes*, and *Tephrodytes*. A list of species examined is presented in Table 2. *Leptobrachium* was chosen as a representative megophryine because it is possibly the most primitive member of that group (Estes, 1970). Character states for *Eopelobates* were determined from the text, figures, and photographs in Estes (1970), Špinar (1972), and Špinar and Roček (1984). Only *E. anthracinus* and *E. bayeri* were considered because the status of other species in this genus has been questioned (Roček, 1981). For *Macropelobates* the character states were determined from examination of the holotype and an undescribed, disarticulated specimen, consisting mostly of postcranial bones, that was discovered in the collections of the American Museum of Natural History by Max K. Hecht. Because this specimen exhibits no differences from the holotype of *Macropelobates*, other than being slightly smaller, I concur with Hecht's identification of it. The descriptions of *Macropelobates* by Noble (1924), Estes (1970), and Roček (1981, 1982) were also used. For *Miopelodytes* character states were ascertained from examination of the holotype. Character states for the remaining anurans were determined through examination of dry skeletons and cleared and stained specimens. In this study *Spea* is treated as a genus, even though it is commonly considered to be a subgenus of *Scaphiopus*, to avoid problems in assigning character states for features in which the two taxa differ. For each character, polarity assessments were based on the outgroup algorithm (Maddison et al., 1984). *Alytes*, *Bombina*, and *Discoglossus* comprised the outgroup. The distribution of character states for the outgroup can be found in Table 3. Some of the characters used in the analysis are new, although the majority of them come from the studies of Zweifel (1956), Kluge (1966), Estes (1970), Špinar (1972), Sanchiz (1978), Roček (1981, 1982), Špinar and Roček (1984), and Cannatella (1985).

Character Analysis.—A total of 25 cranial and postcranial characters were analyzed in this study. These characters are discussed below.

1. Sculpturing commonly occurs on the outer surface of pelobatoid dermal skull bones. Although the style of sculpturing varies (i.e., pits and grooves, pustulose) and the distribution and amount of sculpturing on dermal skull bones varies, only its presence or absence is noted here. *Leptobrachium*, *Spea*, and *Pelodytes* lack sculpturing on dermal skull bones (state 0). Sculpturing (state 1) occurs in *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Tephrodytes*. Taylor (1941) made no mention of whether dermal skull bone sculpturing occurs in *Miopelodytes*. However, the squamosal, which was not identified by Taylor (1941) in his description of the holotype, bears sculpturing on the zygomatic and

Table 2.—List of Recent and fossil specimens examined.

Taxon	Skeleton	Cleared and stained
Recent		
Bombinatoridae		
<i>Bombina bombina</i>		2
<i>Bombina orientalis</i>		2
Discoglossidae		
<i>Alytes obstetricans</i>		2
<i>Discoglossus jeanneae</i>		2
<i>Discoglossus pictus</i>	1	
Pelobatidae		
<i>Leptobrachium hasselti</i>	1	
<i>Leptobrachium montanum</i>	1	
<i>Megophrys monticola</i>	1	1
<i>Pelobates cultripes</i> (adult)	2	2
<i>Pelobates cultripes</i> (tadpole series)		36
<i>Pelobates fuscus</i>		2
<i>Scaphiopus couchi</i>	3	2
<i>Scaphiopus holbrooki</i>	6	
<i>Scaphiopus hurteri</i>	1	
<i>Spea bombifrons</i>	5	2
<i>Spea hammondi</i>	2	
<i>Spea intermontanus</i>	1	
Pelodytidae		
<i>Pelodytes punctatus</i>	2	8
Fossil		
Pelobatidae		
<i>Macropelobates osborni</i>	2	
<i>Scaphiopus skinneri</i>	1	
Pelodytidae		
<i>Miopelodytes gilmorei</i>	1	

otic rami. Poor preservation and their orientation in the matrix prevents the identification of sculpturing on other dermal skull bones.

2. The frontoparietal of pelobatoids is either paired (state 0), consisting of a right and left half, or is tripartite (state 1), being composed of a right and left ossification and a medial ossification situated posterior to them (Roček, 1981, 1988). The frontoparietal is paired in *Leptobrachium*, *Scaphiopus*, *Spea*, *Miopelodytes*, *Pelodytes*, and *Tephrodytes*.

Roček (1981) has documented the tripartite condition in *Pelobates fuscus*, *P. syriacus*, and *Eopelobates bayeri*, and has inferred it for *E. anthracinus* (Špinar and Roček, 1984). I have observed it in cleared and stained tadpoles of *P. cultripes*. Roček (1981) noticed that during the ontogeny of the frontoparietal in *Pelobates* the three ossifications fuse together leaving no trace of a suture. In adults of *Eopelobates bayeri* the median suture is visible although it does not extend to the posterior end of the bone because of the medial ossification (Roček, 1981; Špinar and Roček, 1984).

For *Macropelobates* neither Noble (1924:fig. 1) nor Estes (1970:fig. 27) illustrated a median suture of the frontoparietal. However, Roček (1981) detected a

Table 3.—Distribution of character states among taxa used in the phylogenetic analysis. 0 indicates the primitive state, 1 and 2 derived states, and 9 missing or inapplicable data. Usage of 1 and 2 does not imply consecutively derived states.

	Character numbers																			
	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	2	2	2
	0	1	2	3	4	5	6	7	8	0	1	2	3	4	5	6	7	8	9	0
<i>Leptobrachium</i>	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0
<i>Eopelobates</i>	1	1	1	1	1	1	1	0	9	9	9	1	1	1	1	0	0	1	1	1
<i>Macropelobates</i>	1	0	1	1	9	9	1	9	9	9	1	0	1	1	0	0	9	1	9	1
<i>Pelobates</i>	1	1	1	1	0	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0
<i>Scaphiopus</i>	1	0	1	1	0	1	1	1	2	0	1	1	0	0	1	1	0	1	0	0
<i>Spea</i>	0	0	0	1	0	0	0	1	2	0	1	1	0	0	1	1	0	1	0	0
<i>Miopelodytes</i>	1	0	0	9	9	9	1	0	9	9	9	9	1	0	0	9	9	9	9	0
<i>Pelodytes</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1
<i>Tephrodytes</i>	1	0	1	1	0	1	0	0	9	1	9	1	1	1	0	1	1	0	9	0
<i>Discoglossus</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alytes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bombina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

small notch on the posterior margin of the frontoparietal in *Macropelobates* which is asymmetrical on the dorsal surface and symmetrical on the posterior surface. Because this notch divides the frontoparietal into two symmetrical halves, he suggested that it is paired. I found that in the holotype the median suture can be clearly observed at the posterior end of the frontoparietal, arising from the notch, thereby providing direct evidence for the paired nature of the frontoparietal in *Macropelobates*.

3. In some anurans the two halves of the frontoparietal do not meet along the midline of the skull, which allows exposure of the frontoparietal fontanelle (state 0). This occurs in *Spea*, *Miopelodytes*, and *Pelodytes*. The frontoparietal bones are in contact medially and thus cover the frontoparietal fontanelle (state 1) in *Leptobrachium*, *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Tephrodytes*.

4. The posterolateral corner of the frontoparietal of some pelobatoids is drawn out to a point, the posterior tip (state 1). This occurs in *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, *Spea*, and *Tephrodytes*. *Leptobrachium* and *Pelodytes* lack the posterior tip of the frontoparietal (state 0). The condition in *Miopelodytes* cannot be determined.

5. The anterolateral margin of the nasal of pelobatoids varies in shape, being either concave (state 0), forming the posterior border of the narial opening, or straight (state 1). The margin is concave in *Pelobates*, *Scaphiopus*, *Spea*, and *Tephrodytes*. *Leptobrachium* and *Eopelobates* have a straight margin. Cannatella (1985) considered the anterolateral narial margin in *Pelodytes* to be straight. However, because the specimens that I examined all have a concave margin, I consider the state for *Pelodytes* to be primitive.

In a reconstruction of the skull of *Macropelobates*, Estes (1970) suggested that the anterolateral margin of the nasal is concave. However, this portion of the bone is not preserved (Noble, 1924; Roček, 1982), and thus the shape of the anterolateral margin is unknown. The condition of the nasal in *Miopelodytes* cannot be determined.

6. The zygomatic ramus of the squamosal either does not articulate with the maxilla (state 0), or articulates with the maxilla (state 1). In *Leptobrachium*, *Spea*,

and *Pelodytes* it does not articulate with the maxilla. The squamosal articulates with the maxilla in *Eopelobates*, *Pelobates*, *Scaphiopus*, and *Tephrodytes*. In *Macropelobates* the anterior end of the zygomatic ramus of the left squamosal and the posterior end of the left maxilla are both broken away, thereby eliminating direct evidence of their articulation, or lack thereof. Roček (1982) observed that the dorsal portion of the broken edge of the maxilla is very thick, indicating a strong zygomatic process (processus zygomaticomaxillaris of Roček, 1981), with which the zygomatic ramus of the squamosal articulates. However, the presence of the palatine process at the anterior end of the maxillary fragment indicates that the preserved portion of maxilla formed the ventral border of the orbit. Thus, the thickened bone Roček (1982) believed to be the zygomatic process is actually the orbital margin. Therefore, it cannot be determined if the squamosal articulated with the maxilla in *Macropelobates*. Although Taylor (1941) made no mention of it, a right squamosal, bearing both a zygomatic and otic ramus, is preserved in the holotype of *Miopelodytes*. Unfortunately, it cannot be determined if the zygomatic ramus of the squamosal articulated with the zygomatic process of the maxilla because the bones are not preserved in articulation and the portion of the maxilla where the zygomatic process would be, if present, is covered by a portion of the pterygoid.

7. The otic ramus of the squamosal in lateral view is either a tiny nubbin (state 0) or is slightly elongate and somewhat deep (state 1). The otic ramus is reduced in *Leptobrachium*, *Spea*, *Pelodytes*, and *Tephrodytes*. It is well-developed in *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Miopelodytes*.

8. The quadratojugal is present (state 0) in *Leptobrachium*, *Eopelobates*, *Pelobates*, *Pelodytes*, and *Tephrodytes*. It is absent (1) in *Scaphiopus* and *Spea*. In *Macropelobates* its presence or absence is controversial. Noble (1924) did not mention this bone in his description of *Macropelobates*. Estes (1970) argued for the probable presence of the quadratojugal, as he observed that the maxilla bore a posterior process with which the quadratojugal would articulate. Roček (1982) observed that the posterior end of the maxilla is broken away and that the bone along this break, in the posteroventral corner, is very thin suggesting that the posterior process was absent, and thus the quadratojugal was absent. However, the presence of the palatine process and teeth on the dentary process indicates that the preserved portion of maxilla is from the orbital region and not the posterior end of the maxilla, as suggested by Roček (1982). Because there is no solid evidence for the presence or absence of the quadratojugal, its state is here considered to be unknown. It cannot be determined if the quadratojugal was present in *Miopelodytes*.

9. The postchoanal ramus of the vomer, when present, forms the posterior border of the internal nares. A short postchoanal ramus (state 0) occurs in *Pelodytes*. This ramus is absent (state 1) in *Pelobates* and *Leptobrachium*. *Scaphiopus* and *Spea* possess an elongate postchoanal ramus (state 2) that almost reaches the maxilla. The presence or absence of the postchoanal ramus remains unknown in *Eopelobates*, *Macropelobates*, *Miopelodytes*, and *Tephrodytes* due to the incompleteness of these specimens.

10. In *Pelodytes* and *Tephrodytes* the anterior ramus of the pterygoid is elongate, being greater than twice the length of the medial ramus (state 1). The anterior ramus of the pterygoid is less than twice the length of the medial ramus (state 0) in *Leptobrachium*, *Eopelobates*, *Pelobates*, *Scaphiopus*, and *Spea*. The pterygoid

is incompletely known in *Macropelobates* and *Miopelodytes*. In *Eopelobates* the length of the rami has not been described.

11. The parahyoid bone is present (state 0) in *Pelodytes* and is absent (state 1) in *Leptobrachium*, *Pelobates*, *Scaphiopus*, and *Spea*. It has not been identified for *Eopelobates*, *Macropelobates*, *Miopelodytes*, and *Tephrodytes*. However, this character is considered to be unknown for these anurans because it is impossible to determine whether the parahyoid bone does not occur or was not preserved in these frogs.

12. The neural arch of the presacral vertebrae either barely extends beyond the level of the posterior zygapophyses (state 0) or forms an elongate spine which extends posteriorly beyond the level of the posterior zygapophyses (state 1). *Leptobrachium* and *Pelodytes* have vertebral neural arches that are not elongate. The vertebral neural arches are elongate in *Eopelobates*, *Macropelobates*, *Pelobates*, *Scaphiopus*, *Spea*, and *Tephrodytes*. Unfortunately, this character cannot be assessed in *Miopelodytes* because of damage.

13. The transverse processes of the last two presacral vertebrae of pelobatoids are directed either moderately anteriorly (state 0), or strongly anteriorly (state 1). Those directed moderately anteriorly are not situated close alongside the vertebral centrum and do not reach the level of the anterior zygapophyses of the preceding vertebra. In contrast, those directed strongly anteriorly tend to lie close alongside the vertebral centrum and the tips of the transverse processes almost reach the level of the anterior zygapophyses of the preceding vertebra. *Leptobrachium*, *Macropelobates*, *Scaphiopus*, and *Spea* possess transverse processes with a moderately anterior orientation. They are directed strongly anteriorly in *Eopelobates*, *Pelobates*, *Miopelodytes*, *Pelodytes*, and *Tephrodytes*.

14. In some pelobatoids the sacral diapophyses are expanded (state 0) whereas in others they are widely expanded (state 1). Traditionally, for descriptive and comparative purposes, the length of the sacral diapophyses has been compared to the equivalent number of vertebrae (Zweifel, 1956; Estes, 1970; Roček, 1982). For example, the length of the sacral diapophyses of *Scaphiopus* is equal to the length of two presacral vertebrae whereas those of *Pelobates* are equal to the length of four presacral vertebrae (Zweifel, 1956). This method works well with Recent specimens but is difficult to apply to fossils because the vertebral centra are commonly not exposed or poorly preserved. Instead, for the purpose of this study, sacral diapophyses considered to be expanded are those having a width greater than length. Widely expanded sacral diapophyses are those having a length greater than width. Expanded sacral diapophyses occur in *Leptobrachium*, *Scaphiopus*, *Spea*, and *Miopelodytes*, whereas widely expanded diapophyses occur in *Eopelobates*, *Macropelobates*, *Pelobates*, *Pelodytes*, and *Tephrodytes*.

15. In pelobatoids the scapula is either short (state 0) or long (state 1). The scapula is considered to be short if its length is less than that of the clavicle, and long if its length is greater than that of the clavicle. *Pelodytes* and *Tephrodytes* have a short scapula. It is long in *Leptobrachium*, *Eopelobates*, *Pelobates*, *Scaphiopus*, and *Spea*. In *Miopelodytes* the right scapula is preserved but neither clavicle is preserved. However, when the scapula of *Miopelodytes* is compared to the scapula from a *Scaphiopus* specimen of similar size, it is apparent that the scapula of *Miopelodytes* is short. For *Macropelobates* a similar comparison with *Pelobates* reveals that the scapula is long.

16. Some pelobatoid scapulae bear an anterior lamina (state 0), which is a thin

ridge of bone along the anterior edge of the scapula. An anterior lamina occurs in *Eopelobates*, *Macropelobates*, *Pelobates*, and *Pelodytes*. It is absent (state 1) in *Leptobrachium*, *Scaphiopus*, *Spea*, and *Tephrodytes* (Fig. 7). The presence or absence of the anterior lamina cannot be determined with certainty in *Miopelodytes*.

17. Both *Tephrodytes* and *Pelodytes* bear a small tubercle, the anterior tubercle, at the anterior margin of the ventral end of the scapula (state 1, Fig. 7). *Leptobrachium*, *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Spea* lack the anterior tubercle (state 0). Spinar (1972) makes no mention of this tubercle in his detailed description of the scapula of *E. bayeri*, so it is most likely absent. Unfortunately, the presence or absence of the anterior tubercle cannot be determined for *Miopelodytes* because the scapular bone is so badly damaged.

18. The clavicle either overlaps the scapula anteriorly (state 0) or abuts the scapula's ventral edge, and thus does not overlap it anteriorly (state 1). In Recent pelobatids the scapula is not overlain anteriorly by the clavicle (Lynch, 1973; Trueb, 1973; Duellman, 1975; Duellman and Trueb, 1986). However, some confusion exists as to whether or not the scapula is anteriorly overlain by the clavicle in the pelodytids. Trueb (1973), and Duellman and Trueb (1986) stated that the scapula is not anteriorly overlain by the clavicle, whereas Lynch (1973) and Duellman (1975) pointed out that the scapula is partially overlain by the clavicle. Examination of specimens of *Pelodytes*, in which the clavicle and scapula are in articulation, shows that the scapula is anteriorly overlain by the clavicle. The scapula is anteriorly overlain by the clavicle in *Pelodytes* and *Tephrodytes*, and is not overlain in *Leptobrachium*, *Eopelobates*, *Pelobates*, *Scaphiopus*, and *Spea*. The state of this character cannot be determined in *Macropelobates* and *Miopelodytes*.

19. The medial end of the coracoid is considered to be expanded if the width of the medial end is greater than the width of the lateral end (state 1). It is expanded in *Leptobrachium*, *Eopelobates*, *Macropelobates*, and *Pelobates*. The medial end is not expanded (state 0) in *Scaphiopus*, *Spea*, and *Pelodytes*. The coracoids of *Miopelodytes* and *Tephrodytes* are not known.

20. The sternum is ossified (state 1) in *Leptobrachium*, *Eopelobates*, *Pelobates*, and *Pelodytes*. It is cartilaginous in *Scaphiopus* and *Spea* (state 0). A sternum has not been identified in *Macropelobates*, *Miopelodytes*, and *Tephrodytes*. Possibly an ossified sternum was present but not preserved in these taxa. Therefore the state of this character is considered to be unknown.

21. The ischium does not extend posteriorly beyond the dorsal acetabular expansion of the ilium (state 0) in *Pelobates*, *Scaphiopus*, *Spea*, *Miopelodytes*, *Pelodytes*, and *Tephrodytes*. It does extend posteriorly beyond the dorsal acetabular expansion of the ilium (state 1) in *Leptobrachium*, and *Eopelobates*. Both Zweifel (1956) and Estes (1970) illustrate the ischium of *Macropelobates* as not extending greatly posteriorly. My examination of this genus has convinced me that the ischium does extend greatly beyond the level of the dorsal acetabular expansion. The difference in our interpretations could be because the specimen has been extensively prepared in the time between their study and mine. Also, Estes (1970) reconstructed the pubis as unossified, although Noble (1924) pointed out that it was either ossified or that there was no room for it. This difference in interpretation caused Estes (1970) to orient the ischium somewhat incorrectly, making it appear as though it did not extend posteriorly.

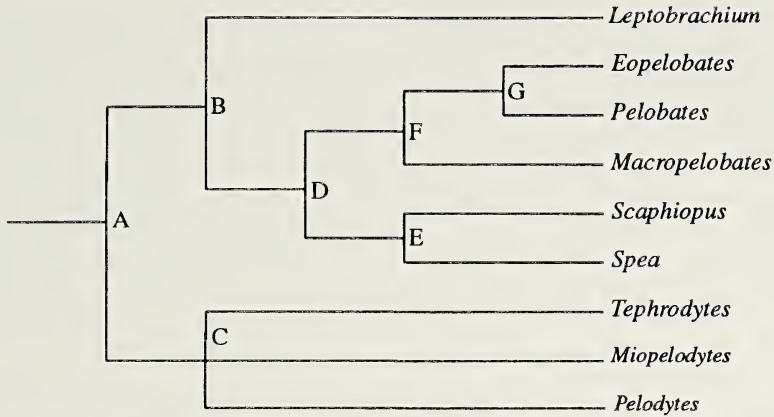


Fig. 9.—Consensus of two phylogenies for the Pelobatoidea. Synapomorphies supporting each node are discussed in the text.

22. Typically, the tibiale and fibulare of adult anurans are fused at their proximal and distal ends (state 0). However, those of *Miopelodytes*, *Pelodytes*, and *Tephrodytes* are completely fused to form a single bone (state 1).

23. Pelobatoids have either three free distal tarsal bones (state 0) in which distal tarsals 1 and 2 are free and distal tarsals 3 and 4 fused, or two free distal tarsal bones (state 1) in which distal tarsal 1 is free and distal tarsals 2, 3, and 4 are fused (Lynch, 1973). *Eopelobates* and *Pelodytes* possess three distal tarsal bones, whereas *Leptobrachium*, *Pelobates*, *Scaphiopus*, and *Spea* possess two. The number of distal tarsal bones is unknown for *Macropelobates*, *Miopelodytes*, and *Tephrodytes*.

24. In some pelobatoids the prehallux is modified as a bony spade which enhances burrowing ability. A spade is absent (state 0) in *Leptobrachium*, *Eopelobates*, *Pelodytes*, *Miopelodytes*, and *Tephrodytes*. It occurs (state 1) in *Macropelobates*, *Pelobates*, *Scaphiopus*, and *Spea*.

25. In *Scaphiopus* and *Spea* the gracilis muscle partially overlaps the sartorius muscle and its tendon, thereby partially concealing these structures (state 1). The gracilis muscle does not partially conceal the sartorius muscle and its tendon in the other extant pelobatoids (state 0). Obviously, the state for this character cannot be determined in the fossil taxa *Eopelobates*, *Macropelobates*, *Miopelodytes*, and *Tephrodytes*.

Results.—Two equally parsimonious trees were generated by PAUP (version 3.0S for Macintosh, Swofford, 1991) utilizing the branch and bound method in which the trees were rooted using the outgroup method. The trees have a length of 54 steps and the consistency index is 0.519. All characters were treated as unordered. Although PAUP was run using both the ACCTRAN and DELTRAN optimizations, the results presented here are based on the trees obtained using the ACCTRAN optimization because it favors reversals. A consensus of the two trees is presented in Fig. 9.

The results of this cladistic analysis differ from those of Cannatella (1985) and Ford and Cannatella (1993). Here, the monophyletic Pelobatoidea is divided into two, well-supported clades, the Pelodytidae and the Pelobatidae. *Tephrodytes* is

a member of the Pelodytidae, but its relationships with *Miopelodytes* and *Pelodytes* are unresolved. The Pelobatidae includes the representative megophryine *Leptobrachium*, *Eopelobates*, *Pelobates*, *Macropelobates*, *Scaphiopus*, and *Spea*. That *Eopelobates* is a member of the Pelobatidae is well-supported. However, because it is most closely related to *Pelobates*, it should be considered a member of the Pelobatinae, thereby making the Eopelobatinae a synonym of the Pelobatinae.

Autapomorphies for the Pelobatoidea were not included in this study because they do not contribute toward resolution of pelobatoid relationships. Thus, the synapomorphies of the Pelobatoidea in this study all exhibit homoplasy and are: anterior lamina of scapula absent (character 16, state 1), which reverses to present (state 0) at Node F and *Pelodytes*; and sternum ossified (character 20, state 1), which reverses to cartilaginous (state 0) in *Scaphiopus* and *Spea*.

The Pelodytidae is united at Node C by three nonhomoplasious characters and one that exhibits homoplasy. These are: anterior ramus of pterygoid elongate (character 10, state 1); scapula with anterior tubercle (character 17, state 1); posterior presacral vertebrae with transverse processes oriented strongly anteriorly (character 13, state 1), which also evolves at Node F; and tibiale and fibulare completely fused (character 22, state 1). There are two equally parsimonious solutions regarding the relationships of the pelodytids, in which *Tephrodytes* is more closely related to either *Miopelodytes* or *Pelodytes*. Acceptance of the former theory stipulates that character 14, sacral diapophyses widely expanded (state 1), evolves at Node C, and reverses to expanded (state 0) in *Miopelodytes*, and that four synapomorphies, all homoplasious, define the *Tephrodytes* + *Miopelodytes* clade. These characters are: sculpturing present on dermal skull bones (character 1, state 1), posterior tips of frontoparietal present (character 4, state 1), zygomatic ramus of squamosal articulates with maxilla (character 6, state 1), and vertebral neural arches elongate (character 12, state 1). All four characters also evolve at Node D, the Pelobatinae, and characters 1 and 6 further undergo reversal in *Spea*. Because the state for characters 4, 6, and 12 cannot be determined in *Miopelodytes*, one derived character, presence of dermal skull bone sculpturing, actually supports the association between *Tephrodytes* and *Miopelodytes*. On the other hand, acceptance of the hypothesis that *Tephrodytes* and *Pelodytes* are more closely related is supported by one character, sacral diapophyses widely expanded (character 14, state 1). Assuming this relationship, three characters evolve in *Tephrodytes* that also evolve in the pelobatines (Node D) and are: posterior tips of frontoparietal present (character 4, state 1), squamosal articulates with maxilla (character 6, state 1), and vertebral neural arches elongate (character 12, state 1). Furthermore, the presence of dermal skull bone sculpturing evolves at Node A, the Pelobatoidea, and reverses to absent (state 0) in *Pelodytes*. Resolution of this trichotomy probably cannot be accomplished without further knowledge of *Miopelodytes* and *Tephrodytes*.

The Pelobatidae, united at Node B by four nonhomoplasious and four homoplasious characters, contains two subfamilies: the Pelobatinae (Node D) and the Megophryinae (*Leptobrachium*). Although *Eopelobates* has recently been removed from the Pelobatoidea (Ford and Cannatella, 1993), been placed in its own subfamily, the Eopelobatinae (Špinar, 1972), and has been considered to be close to the megophryines (Zweifel, 1956; Kluge, 1966) or intermediate between the megophryines and pelobatines (Estes, 1970; Špinar, 1972), this study establishes *Eopelobates* as a member of the family Pelobatidae, and the subfamily Pelobatinae.

The Pelobatidae is a monophyletic group that shares four nonhomoplasious and four homoplasious derived characters. The nonhomoplasious synapomorphies are: postchoanal ramus of vomer absent (character 9, state 1), parahyoid bone absent (character 11, state 1), scapula long (character 15, state 1), and scapula not anteriorly overlain by clavicle (character 18, state 1). Of these, however, character 15 is the only one that is known for all members of the Pelobatidae. Other characters supporting this clade are: frontoparietal fontanelle covered by frontoparietals (character 3, state 1), which also evolves in *Tephrodytes*; medial end of coracoid expanded (character 19, state 1), which reverses to not expanded at Node C; ischium extends posteriorly (character 21, state 1), which reverses in *Pelobates* and Node C; and two free distal tarsal bones (character 23, state 1), which reverses to three free distal tarsal bones in *Eopelobates*.

Containing two clades, *Scaphiopus* and *Spea* in one, and *Eopelobates*, *Pelobates*, and *Macropelobates* in the other, the Pelobatinae (Node D) is supported by five synapomorphies, all of which exhibit some degree of homoplasy. Three of these evolve convergently in *Tephrodytes* and are: posterior tips of frontoparietals present (character 4, state 1), squamosal articulates with maxilla (character 6, state 1), and vertebral neural arches elongate (character 12, state 1). The remaining characters are: otic ramus of squamosal present (character 7, state 1), which also evolves in *Miopelodytes* and reverses to reduced in *Spea*; and spade present (character 24, state 1), which reverses to absent in *Eopelobates*.

The clade of *Scaphiopus* and *Spea* (Node E) is defined by six synapomorphies, of which half exhibit no homoplasy. These are: quadratojugal absent (character 8, state 1); postchoanal ramus of the vomer elongate (character 9, state 2); medial end of coracoid not expanded (character 19, state 0); sternum cartilaginous (character 20, state 0); ischium not extended posteriorly (character 21, state 0); and sartorius muscle and associated tendon concealed, in part, by gracilis major (character 25, state 1). Characters 19 and 21 have undergone reversal from the derived state at Node B and character 20 reverses from the derived state at Node A.

Eopelobates, *Pelobates*, and *Macropelobates* form a clade supported by two synapomorphies: sacral diapophyses widely expanded (character 14, state 1), which also evolves in *Tephrodytes* and *Pelodytes*; and anterior lamina of scapula present (character 16, state 0), a reversal from absent at Node A. *Pelodytes* also possesses an anterior lamina of the scapula. The association of *Macropelobates* with *Eopelobates* and *Pelobates* counters Roček's (1982) hypothesis that *Macropelobates* is closest to *Scaphiopus*. The basis of his conclusion was that *Macropelobates* shares 13 characters with *Scaphiopus* and only four with *Pelobates*. However, he was unable to determine the primitive state from the derived state for many of his characters. What Roček (1982) considered to be advanced specializations shared between *Macropelobates* and *Scaphiopus* are: lack of quadratojugal, and proportions of squamosal. A quadratojugal was not preserved with the holotype of *Macropelobates*, which has an incomplete and somewhat disarticulated skull, and Roček (1982) inferred that it was absent. However, I concluded that the presence or absence of a quadratojugal could not be determined for *Macropelobates* (see Character Analysis, character 8). This leaves the proportions of the squamosal as Roček's (1982) only synapomorphy between *Macropelobates* and *Scaphiopus*. Of the four characters shared between *Macropelobates* and *Pelobates*, Roček (1982) was unable to determine whether they were primitive or derived. In this study only two of the five synapomorphies for *Scaphiopus* and *Spea* could be determined in *Macropelobates*. These are: medial end of coracoid expanded (character 19,

state 1), and ischium expanded posteriorly (character 21, state 1). Both *Scaphiopus* and *Spea* possess the primitive state for these characters, which represents a reversal. Thus, based on the characters analyzed in this study, *Macropelobates* is more closely related to *Eopelobates* and *Pelobates* than to *Scaphiopus* and *Spea*. However, additional knowledge about *Macropelobates* may lead to a different hypothesis of relationship.

Two synapomorphies define the clade of *Eopelobates* and *Pelobates* (Node G): frontoparietal derived from three ossifications (character 2, state 1); and transverse processes of posterior presacral vertebrae oriented strongly anteriorly (character 13, state 1), which also evolves in the pelodytids. Milner (1988) was correct in his assumption that a frontoparietal derived from three ossifications was merely a synapomorphy for a clade within the Pelobatidae and not indicative of a separate origin for *Eopelobates* and *Pelobates* from other anurans as proposed by Roček (1981).

DISCUSSION

Examination of *Tephrodytes*, which has the diagnostic pelodytid character of a fused tibiale and fibulare, revealed there are several derived characters that also occur in some pelobatids, but not in *Pelodytes*. Thus, it seemed possible that these characters would support inclusion of the pelodytids in the Pelobatidae, and that *Pelodytes* possesses the primitive state for these characters as a result of reversal. However, the phylogeny (Fig. 9) derived from this cladistic analysis suggests that pelodytids are the sister group to the clade including the megophryines and pelobatines. Thus, it is best to retain the pelodytids in their own family. Derived characters that occur in both *Tephrodytes* and the pelobatines, including *Eopelobates*, are the result of convergence. These characters are: posterior tip of frontoparietal present (character 4), zygomatic ramus of squamosal articulates with maxilla (character 6), and presacral vertebral neural arches elongate (character 12). Furthermore, a concealed frontoparietal fontanelle evolved convergently in *Tephrodytes* and the pelobatids. Note, however, that in *Spea* the frontoparietal fontanelle is exposed, a reversal. Ford and Cannatella (1993) listed the fused tibiale and fibulare as the only unambiguous synapomorphy for the Pelodytidae. To this I add the following: anterior ramus of pterygoid elongate, and scapula with anterior tubercle.

The Pelobatidae, used here in its traditional sense to include the megophryines and pelobatines, is monophyletic. Although numerous characters support this relationship, none of them are unique to pelobatids. Three of the characters supporting the Pelobatidae that exhibited no homoplasy in this study also evolved in the Neobatrachia: parahyoid bone absent, scapula long, and scapula not overlain anteriorly by clavicle. All of the characters supporting the Pelobatinae exhibit some degree of homoplasy. This is caused, in part, by several of these features evolving convergently in *Tephrodytes*, and also by the loss of the spade in *Eopelobates*. That *Eopelobates*, used here to include *E. anthracinus* and *E. bayeri*, is a member of the Pelobatinae is well-supported, thereby making the Eopelobatinae a synonym of the Pelobatinae. One unique character, frontoparietal derived from three ossifications, supports the close relationship between *Eopelobates* and *Pelobates*. *Macropelobates* is the sister taxon to this clade, but there are no characters unique to this clade. Within this study three nonhomoplasious characters support the clade of *Scaphiopus* and *Spea*. Of these only one, sartorius muscle and associated tendon partially concealed by gracilis major, appears to be unique. The

elongate postchoanal ramus of the vomer also occurs in the rhinophrynid, *Chelomophrynus*, and the quadratojugal has also been lost in *Ascaphus*, *Leiopelma*, and *Notobatrachus*.

In conclusion, a phylogeny for the Pelobatoidea is provided. This phylogeny follows the more traditional approach in that the pelobatids and pelodytids are sister clades and the megophryines are included in the Pelobatidae. Relationships within the Pelodytidae are unresolved, and more information on the extinct members is required. Within the Pelobatidae, the relationships of *Eopelobates* and *Macropelobates* as presented here differ from previous phylogenetic hypotheses. However, additional knowledge of these taxa could result in a different phylogeny.

ACKNOWLEDGMENTS

I am grateful to the following for loan of specimens in their care: the late C. J. McCoy, CM; N. Hotton III, USNM; R. Hunt, USNM; D. Miao, KU; M. C. McKenna, AMNH; and H. Voris, FMNH. Illustrations in Figures 4 and 5 were skillfully prepared by A. D. Redline. Thanks are due to D. Baird for his assistance in coining the specific name, and to M. Hecht who brought the second only known specimen of *Macropelobates* to my attention. This investigation benefitted from discussion with F. B. Sanchiz. K. C. Beard and J. E. Rawlins provided assistance with running PAUP, and A. Campbell provided technical assistance. The late C. J. McCoy, who read an earlier version of this manuscript, D. C. Cannatella, and an anonymous reviewer provided helpful comments for which I am grateful. This research was supported in part by the M. Graham Netting Research Fund.

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TAIWANESE SPECIES OF *NEOPANORPA*
(INSECTA: MECOPTERA: PANORPIDAE)GEORGE W. BYERS¹

ABSTRACT

Neopanorpa youngi n. sp. is described and illustrated. It is compared in detail with *N. ophthalmica* Navas and *N. gradana* Cheng. All known Taiwanese species of *Neopanorpa* are differentiated in separate keys for males and females, and all are illustrated by taxonomic details.

INTRODUCTION

Taiwan (formerly Formosa) has a surprisingly rich fauna of Mecoptera, including numerous species of *Panorpa* and fewer of *Neopanorpa* and *Bittacus*. The island has an area of nearly 36,000 km² (13,836 sq mi). Except for an alluvial plain about 30 km wide along its western side, it is largely mountainous, much of its area above 1500 m and several peaks rising above 3500 m. But Taiwan is crossed at midlength by the Tropic of Cancer. As a result, it has a diversity of habitats, ranging from lowland tropical rain forest to high montane forest and grassland. This has undoubtedly influenced the variety of its insect fauna.

Neopanorpa includes approximately 95 species at present, all in southeastern Asia. The ranges of species seldom overlap, but I suspect this is due to insufficient collecting. Species of *Neopanorpa* occur in India, Nepal, Bhutan, and Sikkim, eastward through Burma, Thailand, Laos, and Vietnam to southern China, chiefly south of 35° latitude, and southeastward through peninsular Malaysia to Sumatra, Java, and Borneo. Much of this composite range overlaps that of the more boreal genus *Panorpa*.

In *Neopanorpa*, the wings are more slender, particularly near their bases, than in *Panorpa*. Vein 1A in the fore wing is relatively short (around 25% of wing length) and ends at the wing margin before the level of the origin of the radial sector (ORs). In *Panorpa*, 1A extends well beyond the level of ORs and is often more than 40% as long as the entire fore wing. There are correlated differences in both male and female genital structures as well, but these are not easily described in this limited treatment.

The genus *Neopanorpa* is represented in Taiwan by at least nine species. Navás (1911) named two of these as *Campodotecnum formosanum* and *C. ophthalmicum*; but Enderlein's genus *Campodotecnum* was subsequently relegated to the synonymy of *Neopanorpa* (Esben-Petersen, 1913). In 1912, Esben-Petersen described *Panorpa sauteri*, which was later transferred to *Neopanorpa*. Issiki (1927) added *N. makii* and *N. magna*; and Issiki and Cheng (1947) described *N. dispar*. Cheng (1952) named *N. gradana* and *N. k-maculata*. On a recent collecting trip to Taiwan, Dr. C. W. Young found the ninth species, described here.

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Submitted 13 July 1993.

Neopanorpa youngi, new species

Description based on four males, three females, pinned.

Head. — Dorsum mostly piceous from area around ocelli backward onto occiput; dark yellowish brown along margins of eyes. Rostrum amber-brown; mouthparts yellowish brown except tips of maxillary palpi black. Scape and pedicel yellowish brown, flagellum brown to dark brown, with 42–44 flagellomeres (number may vary in one individual). Antennal length about 12–13 mm.

Thorax. — Pronotum unevenly dull yellowish brown, with diffuse black medial band. Mesonotum and metanotum mostly sordid yellowish brown, with piceous medial stripe that widens abruptly across anterior mesonotum. Pleural areas, coxae, and mera dull pale yellowish brown, with small, darkly sclerotized spots at coxal articulations and below wing bases. Hairs of pleura short and pale, longer on anterior surfaces of middle and hind coxae. Legs yellowish brown; tarsi darkening gradually to brown on apical tarsomeres.

Wings strongly tinged with yellowish brown, bands and spots brown. Apical band enclosing one or two small to large pale areas. Pterostigmal band complete, branched posteriorly near midlength; a slender, irregular, diagonal band connecting inner (basal) branch of pterostigmal band to marginal spot. Basal band entire (holotype) or interrupted near M, connected in some individuals by slender, diagonal band to marginal spot.

Abdomen of Male. — Terga 2–4 mostly black; posterior prolongation of tergum 3 (part of notal organ) dark yellowish brown, highly arched dorsad (Fig. 4); median elevation on tergum 4 black, bluntly bilobed, with hairs directed cephalad. Tergum 5 and segment 6 unevenly dark yellowish brown; sterna 2–5 pale yellowish brown. Segments 7–9 yellowish brown except for brown shading on sides of hypovalves. Ninth tergum distinctly bilobed at apex (Fig. 7), extending far beyond ends of basistyles (Fig. 3). Ninth sternum wide in ventral aspect, about 80% of greatest width of genital bulb measured across basistyles. Hypovalves (Fig. 1) narrowly rounded apically, appearing nearly acute, mesal edges rolled at base; blunt lobe on dorsal surface of each (Fig. 2) extending between basistyles, thus not evident in lateral aspect (Fig. 3). Dististyles slender, not strongly curved toward apex, each with sharply tipped inner basal lobe (Fig. 5). Aedeagus (Fig. 6) with two strongly bowed ventral appendages approximately in position of ventral parameres (but possibly homologous with branches from parameres forming aedeagal hamulus in *Panorpa*; see Byers, 1993), each terminating in pale, wrinkled lobe directed abruptly laterad at nearly right angle to bowed part of appendage. Ventral valves strigose; lateral processes continuous with ventral parameres; dorsal parameres inclined together, with uneven, almost truncate ends.

Abdomen of Female. — Terga 2–5 piceous-black, corresponding sterna pale yellowish brown; tergum 6 dark yellowish brown, following segments yellowish brown. Well-developed laterotergites on segments 7 and 8. Cerci (Fig. 22) two-segmented, apical segment about three times as long as basal one. Subgenital plate (Fig. 21) notched apically, with median basal membranous indentation; most hairs short, 10–12 long marginal and apical setae. Genital plate (Fig. 19, 20) with short oval axial portion bearing thick, darkened lateral lobes conspicuously expanded dorsad; spatulate arms subparallel.

Body length, male, about 13–14.5 mm (holotype 13 mm); female about 12–13 mm (allotype 13 mm). Length of fore wing, male, 13.9–15.3 mm (holotype 13.9 mm); female 13.2–15.0 mm (allotype 15.0 mm).

Holotype, male, "Taiwan: Kaohsiung, Shanping. 640 m., 11–20 April 1988, J.

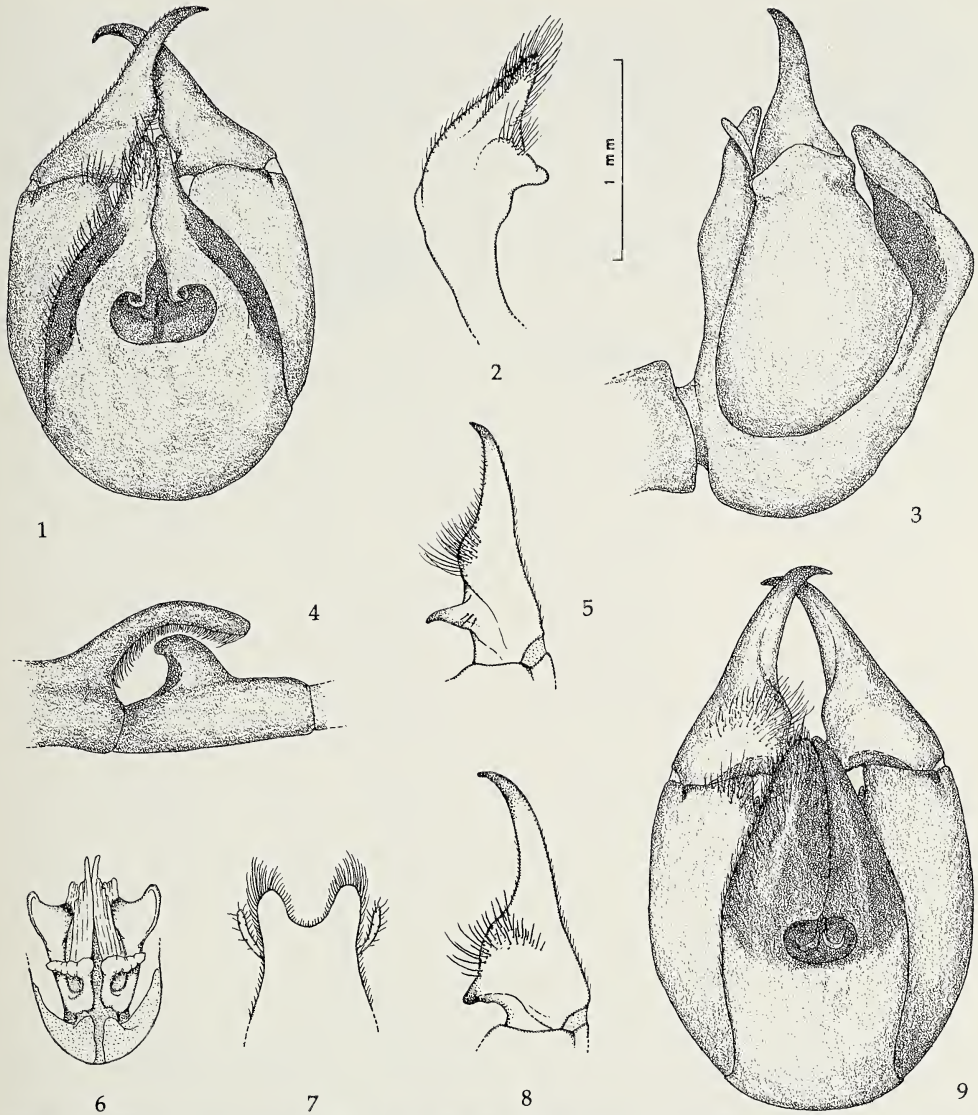


Fig. 1-7.—*Neopanorpa youngi*, n. sp. 1, genital bulb, male paratype, ventral aspect. 2, right hypovalve, male, right lateral aspect. 3, genital bulb, paratype, left lateral aspect. 4, notal organ of abdominal terga 3 and 4, left lateral aspect. 5, right dististyle, male, ventral (and slightly lateral) aspect. 6, aedeagus, male paratype, ventral aspect. 7, ninth abdominal tergum, male, dorsal aspect (diagrammatic). Fig. 8-9. *Neopanorpa ophthalmica*, male syntype (Museum of Zoology, Barcelona). 8, right dististyle, ventral aspect. 9, genital bulb, ventral aspect. Scale: Fig. 1-3, 5-9.

Rawlins, C. Young, R. Davidson." Allotype, two female and one male paratypes, same data as holotype; one male paratype same locality but 21-30 April 1988, C. Young, R. Davidson, J. Rawlins; one male paratype same locality but 1-10 May 1988, R. Davidson, C. Young, J. Rawlins. Holotype, allotype, one male and two female paratypes in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; two male paratypes in the Snow Entomological Museum, Univer-

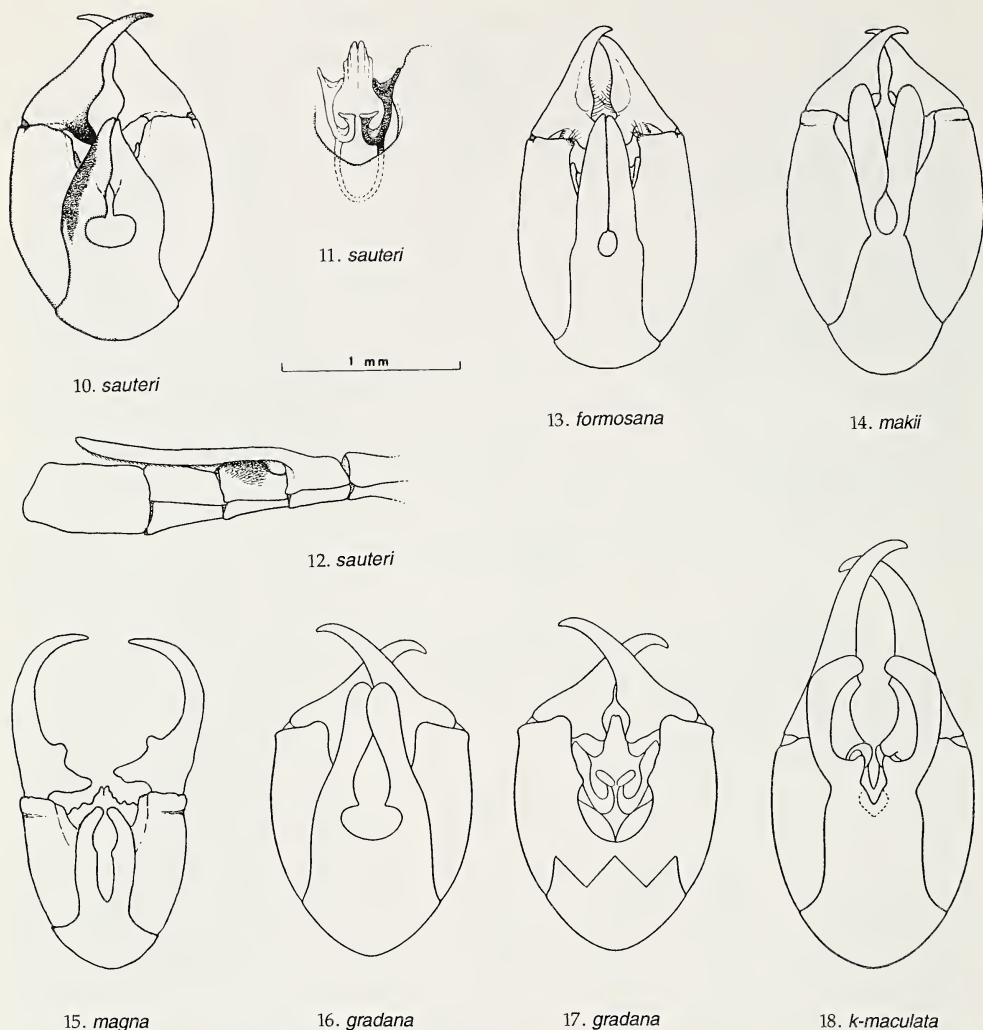


Fig. 10-18.—Taxonomic details of males of Taiwanese species of *Neopanorpa*. 10, genital bulb, *N. sauteri*, ventral aspect. 11, aedeagus, *N. sauteri*, ventral aspect. 12, abdominal segments 2-6, male holotype of *N. sauteri* (Deutsches Entomologisches Institut, Berlin-Friedrichshagen), right lateral aspect, anterior at right (genital bulb missing). 13, genital bulb, *N. formosana*, male syntype (Museum of Zoology, Barcelona), ventral aspect. 14, genital bulb, *N. makii*, after Issiki 1927. 15, genital bulb, *N. magna*, after Issiki 1927. 16, genital bulb, *N. gradana*, from Cheng 1952. 17, same, with hypoalves removed to show aedeagus, from Cheng 1952. 18, genital bulb, *N. k-maculata*, from Cheng 1952. Scale: Fig. 10-13.

sity of Kansas, Lawrence, Kansas. The holotype is intact; the allotype is missing the apical one-third of the right antenna, and its terminal abdominal segments are dissected and mounted in polyvinyl alcohol, on the pin with the specimen.

This species is named for my friend and former student, Dr. Chen-Wen Young of the Carnegie Museum of Natural History, who collected most of the specimens. A native of Taiwan, Dr. Young is an outstanding field entomologist and collector and a very capable taxonomist of Tipulidae.

Neopanorpa youngi superficially resembles *N. ophthalmica*, particularly in wing

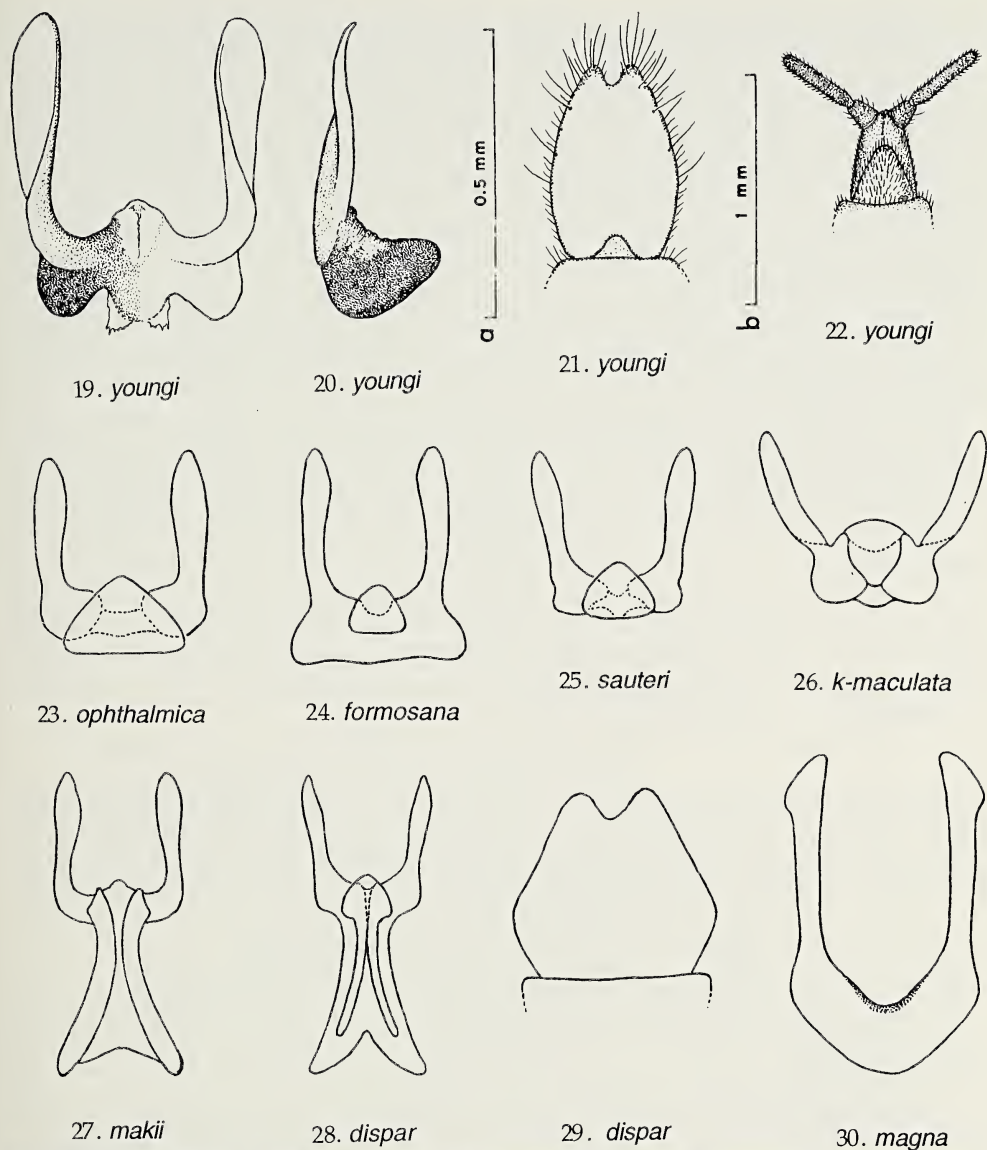


Fig. 19–30.—Taxonomic details of females of Taiwanese species of *Neopanorpa*. 19, genital plate, female allotype of *N. youngi*, n. sp., ventral aspect. 20, same, right lateral aspect. 21, subgenital plate, allotype of *N. youngi*, ventral aspect. 22, terminal abdominal segment and cerci, allotype of *N. youngi*, ventral aspect. 23, genital plate, *N. ophthalmica*, ventral aspect. 24, same, *N. formosana*. 25, same, *N. sauteri*. 26, same, *N. k-maculata*. 27, same, *N. makii*. 28, same, *N. dispar*. 29, subgenital plate, *N. dispar*, ventral aspect. 30, genital plate, *N. magna*, ventral aspect. Fig. 23–30 after Issiki and Cheng 1947. Scale a—Fig. 19, 20; scale b—Fig. 21, 22.

pattern and the subtriangular shape of the male's hypovalves. The hypovalves in *ophthalmica*, however, are wider, less acutely tipped, uniformly dark and with more and longer hairs than those of *youngi*. A conspicuous difference in the genital bulb of the males is with the width of the ninth sternum (hypandrium) in ventral

aspect (Fig. 1, 9). In *youngi*, the width of the sternum is approximately 80% of the greatest width of the genital bulb measured across the basistyles, while in *ophthalmica* it is only about 50–55% (but nearly 68% in *N. gradana*). Differences between *youngi* and both *ophthalmica* and *gradana* include the inner basal lobe of the dististyle, sharply acute in *youngi* but relatively blunt in *ophthalmica* (Fig. 8) and *gradana* (Fig. 17), and the apex of the ninth tergum, with distinct lobes separated by a U-shaped emargination in *youngi* but only shallowly indented, virtually truncate in *ophthalmica* and *gradana*, thus without lobes. In aedeagal structure, *youngi* resembles *sauteri* and *gradana* (compare Fig. 6, 11, and 17). The most obvious difference is in the up-curved ventral appendages I interpret as ventral parameres, the ends of which are enlarged, directed laterally, and pale in *youngi* but flat and disc-like in *sauteri* (actually widened slightly ventrad, or caudad). Cheng (1952) described the distal ends of these appendages in *gradana* (Fig. 17) simply as “broad lobes.”

Females of *N. youngi* differ from those of all other known Taiwanese species in the genital plate, particularly the large, blackened dorsal swelling at each side, at the bases of the posterior arms. Cheng (1952) described somewhat similar structures in *N. k-maculata* as “black and stout,” but I cannot interpret his illustration (Fig. 26) in more detail. Such basal enlargements are not mentioned in the descriptions of other species. The ovoid shape of the axial portion of the plate is also not seen in other Taiwanese species. The apically notched subgenital plate (Fig. 21) of *N. youngi* is scarcely different from its counterpart in several other species; the membranous medial area at the base has not been mentioned or illustrated for other species.

SPECIES IDENTIFICATION

Since I have not seen specimens of some species of *Neopanorpa* from Taiwan, I have relied on descriptions and illustrations provided by S. Issiki and F. Y. Cheng. A few figures drawn by Dr. Cheng have in fact been copied directly from his paper in *Psyche*, with permission of the current editor, Dr. David Furth.

KEY TO MALES OF TAIWANESE *NEOPANORPA*

(Note: Male of *N. dispar* Issiki and Cheng is unknown.)

1. Hypovalves long-elliptical in ventral aspect, slightly overlapped medially (Fig. 13, 14) 2
- 1'. Hypovalves subtriangular in ventral aspect, or rounded at apex, overlapped medially or apically or not overlapped 3
- 2(1). Apical band on fore wing connected to pterostigmal band along costal margin *formosana* Navás
- 2'. Apical band on fore wing narrowly connected to pterostigmal band along vein R_3 *makii* Issiki
- 3(1'). Hypovalves not overlapped, either medially or apically 4
- 3'. Hypovalves overlapped along mesal edges or at apex 5
- 4(3). Hypovalves long, extending far beyond ends of basistyles, bowed laterad (Fig. 18), with small mesal lobe near base of each; sternum 9 prolonged so that hypovalves originate shortly before ends of basistyles; dististyles only slightly curved, outer margins shallowly concave *k-maculata* Cheng
- 4'. Hypovalves short, almost straight, without mesal lobe near base, their apices slightly narrowed and inclined mesad; sternum 9 not prolonged,

- hypoalves terminating near level of ends of basistyles; dististyles (Fig. 15) longer than basistyles, strongly bowed outward (laterad) *magna* Issiki
- 5(3'). Ninth abdominal tergum (epiandrium) shallowly emarginate apically, almost truncate 6
- 5'. Ninth abdominal tergum distinctly bilobed, with lobes separated by deep U-shaped emargination 7
- 6(5). Hypoalves nearly acute at apex, subtriangular in ventral aspect, overlapped slightly along most (about 70%) of their length *ophthalmica* Navás
- 6'. Hypoalves rounded at apex, narrower at midlength than at apex, overlapped only apically for about 30% of their length (Fig. 16) *gradana* Cheng
- 7(5'). Median projection from third abdominal tergum (notal organ) extending over terga 4, 5, and most of 6 (Fig. 12); inner basal lobe of dististyle blunt at apex *sauteri* Esben-Petersen
- 7'. Median projection from third abdominal tergum extending only over two-thirds of tergum 4; apex of inner basal lobe of dististyle acutely pointed *youngi*, n. sp.

KEY TO FEMALES OF TAIWANESE *NEOPANORPA*

(Note: Female of *gradana* Cheng is unknown; its position in this key is based mainly on the wing pattern of the male.)

1. Marginal spot in fore wing not extended to join basal (proximal) branch of pterostigmal band 2
- 1'. Marginal spot in fore wing extended diagonally across wing to join basal branch of pterostigmal band 6
- 2(1). Genital plate with well-developed anterior apodemes (Fig. 27, 28) ... 3
- 2'. Genital plate without evident anterior apodemes 4
- 3(2). Length of subgenital plate of eighth sternum approximately equal to its greatest width (Fig. 29) *dispar* Issiki and Cheng
- 3'. Length of subgenital plate about 1.3 times its greatest width *makii* Issiki
- 4(2'). Apical band of fore wing including extensive pale spots from cell R₂ to cell M₁; wing markings grayish brown *gradana* Cheng
(see Note above)
- 4'. Apical band entire or including only small pale spots; wing markings dark brown to blackish brown 5
- 5(4'). Genital plate without distinct axial portion, arms abruptly widened subapically (Fig. 30); body largely black *magna* Issiki
- 5'. Genital plate with distinct axial portion (Fig. 24); arms gradually widened subapically; body color mainly brown *formosana* Navás
- 6(1'). Band of pigment from marginal spot to pterostigmal band broad with rather even edges, narrowest part as wide as distance between M₁₊₂ and M₃ where bands join *k-maculata* Cheng
- 6'. Connection between marginal spot and pterostigmal band of varying widths but mostly slender, with irregular edges 7
- 7(6'). Axial portion of genital plate broadly triangular in ventral aspect (Fig. 23, 25) 8
- 7'. Axial portion of genital plate ovoid (Fig. 19) *youngi*, n. sp.

- 8(7). Arms of genital plate (apical plate) slightly divergent (Fig. 25); axial portion narrower than distance between arms . . . *sauteri* Esben-Petersen
 8'. Arms of genital plate approximately parallel (Fig. 23); axial portion wider than distance between arms *ophthalmica* Navás

ACKNOWLEDGMENTS

I am indebted to my late friend and colleague Dr. Syûti Issiki and to Dr. Fung Ying Cheng for providing certain descriptions and illustrations of some species of *Neopanorpa*.

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16 SEPTEMBER 1994

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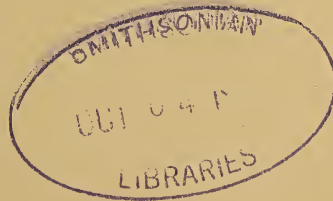
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ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

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BIOLOGY AND IMMATURE STAGES OF CHLOROPIDAE
(INSECTA: DIPTERA) ASSOCIATED WITH SPIKE-RUSHES
(CYPERACEAE: *ELEOCHARIS*) I. STEM BORERS

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ABSTRACT

The life cycles and larval feeding habits of one species of *Chlorops* (*C. obscuricornis* Loew) and three species of *Diptotoxa* [*D. inclinata* Becker, *D. nigripes* (Coquillett), and *D. sp. near versicolor* (Loew)] associated with spike-rushes of the genus *Eleocharis* (Cyperaceae) are presented. Larvae of the four species show resource partitioning by attacking either stems or rhizomes, by feeding at different times, or by utilizing different species of *Eleocharis*.

This study compares the morphology of the larvae; describes and illustrates the eggs, three larval instars, and puparia of three species of *Diptotoxa*; and provides a key separating the third-instar larvae of all four species of *Eleocharis* stem borers.

INTRODUCTION

The sedge genus *Eleocharis*, containing about 150 species in the world, is nearly cosmopolitan in distribution and is particularly well-represented in warmer regions. It is easily distinguished from other genera of Cyperaceae by the presence of a single, terminal, spike-like inflorescence that lacks obvious subtending bracts. Both annual and perennial species occur. Determining species is difficult, as well-developed seed heads and achenes are necessary for identification (Gleason, 1963; Braun, 1967; Scoggan, 1978). Species of *Eleocharis* frequently form nearly pure stands in open wetlands, perhaps due to their ability to secrete compounds that inhibit the growth of other hydrophytic plants (Wooten and Elakovich, 1991).

The importance of spike-rushes to chloropid flies was indicated by Todd and Foote (1987) who reported that a stand of *E. smallii* Britton contained ten of the 22 species of Chloropidae collected in eight vegetation types occurring in a freshwater marsh near Kent, Ohio.

Chlorops, a member of the subfamily Chloropinae, is the largest chloropid genus in North America, containing 35 species (Sabrosky, 1987). Most of the available information on the biology of the genus is based on studies of the gout fly, *C. pumilionis* Bjerkander (*C. taeniopus* Meigen, *auct.*), an economically important pest of cereal grains in Europe. The stem-boring larvae of that species were described in detail by Frew (1923a, 1923b), Balachowsky and Mesnil (1935), Goodliffe (1939, 1942), Nye (1958), and Dennis (1961). Other European species that are stem borers of grasses are *C. speciosa* Meigen, *C. brevimana* Loew, *C. interrupta* Meigen, and *C. marchali* Mesnil (Ferrar, 1987). A few species of Nearctic *Chlorops* have larvae that are primary invaders of sedge stems (Valley et al., 1969). Recently,

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Submitted 19 April 1993.

Rogers et al. (1991) elucidated the life history and described the immature stages of *C. certimus* Adams, a species whose larvae attack stems of the sedge genus *Carex*.

Diptotoxa, also a member of the subfamily Chloropinae, is a cosmopolitan genus that has been recorded in nearly all the biogeographic regions. Five of the seven Nearctic species, *D. alternata* (Loew), *D. inclinata* Becker, *D. messoria* (Fallén), *D. recurva* (Adams), and *D. versicolor* (Loew), are practically transcontinental in distribution; *D. unicolor* Becker is restricted to the western states and provinces; and *D. nigripes* (Coquillett) occurs only in the eastern and midwestern states and provinces (Sabrosky, 1965).

Few papers have been published on the larval feeding habits and host plants of *Diptotoxa*. Wendt (1968) reported that larvae of *D. messoria* are phytophagous in European species of *Eleocharis*, but gave no information concerning host plant specificity, larval feeding habits, or life cycle parameters. Valley et al. (1969) reared *D. messoria*, *D. nigripes*, and *D. sp.* (near *D. inclinata*) from stems of *Eleocharis* in North America. Spencer (1977) reared a New Zealand species from inflorescences of a grass of the genus *Echinochloa*. No immature stage of any species has been described (Ferrar, 1987).

The present paper elucidates the life cycles and larval feeding habits of one species of *Chlorops* and three of *Diptotoxa* that attack the stems and rhizomes of *Eleocharis* spp. in northeastern Ohio. The immature stages of three species of *Diptotoxa* are described and illustrated, and a key is given to the third instars of all four species of *Eleocharis* stem borers. In addition, certain morphological structures found in the larvae are compared.

MATERIALS AND METHODS

Collecting Techniques.—Adults were collected weekly by sweeping vegetation of suitable habitats with a standard aerial insect net. Collecting sites were all located in Portage County in northeastern Ohio. Eggs were collected in nature by pulling up *Eleocharis* plants in the field and examining them in the laboratory. Larvae and puparia were found during the winter and spring by examining developing rhizomes, the bases of young shoots, and new stems of *Eleocharis* that were approximately 0.5–1.0 m in height.

Rearing Techniques.—Adult flies were sexed and paired, and placed in baby food jars (9 × 6 cm) which had their bottoms removed. The jars were inverted, and the top pressed into the bottom of a small plastic Petri dish (5.5 × 1.3 cm) containing moist peat moss. The open bottom of the jar was covered with 1–4 layers of cheesecloth held in place by a rubber band. A small pellet of honey and brewer's yeast pressed to the side of the jar served as adult food. The peat moss was moistened daily, and the fly food replaced periodically. Small sections of *Eleocharis* stem, approximately 5–6 cm in length, were oriented vertically in the peat moss to provide oviposition sites. These were replaced periodically with fresh sections, as females would not oviposit on decomposed material.

Eggs removed from the rearing jars were placed in small Petri dishes (5.4 × 1.3 cm) containing discs of moist paper toweling; occasionally whole stem sections containing eggs were transferred.

Newly-hatched larvae were placed on young shoots of *Eleocharis* and examined daily for information on larval feeding habits, length of larval stadia, and sites of pupation. Larvae were transferred to fresh plant material regularly, as they quickly abandoned decaying stems. Puparia were transferred to small Petri dishes containing moist peat moss. Parasitoid wasps emerging from puparia were killed and preserved in 70% ETOH.

Preservation and Preparation of Specimens.—Approximately 10–20 eggs of each species were measured and preserved in KAAD. Larvae were killed in hot (not boiling) water and were either preserved in 70% alcohol or treated for further study, and drawn using standard light microscopy techniques.

Abbreviations used in figures are: A, antenna; AP, anterior papilla; APB, anterior end of parastomal bar; ApT, apical tooth; ASL, anal slit; ASp, anterior spiracle; AT, accessory tooth; Cph, cephalopharyngeal skeleton; DC, dorsal cornu; FP, frontal papilla; GP, genal papilla; HS, hypopharyngeal sclerite; IP, interspiracular process; LP, lateral papilla; LS, ligulate sclerite; m, membrane; MH, mouth-hooks; MP, maxillary palp; Pa, papilla; PB, parastomal bar; PcS, pseudocephalic segment; Pfp, pre-

frontal papilla; PhS, tentoropharyngeal sclerite; PP, perianal pad; PSP, posterior spiracular plate; R, ramus; SB, spinule band; ShS, subhypopharyngeal sclerite; SSL, spiracular slit; StB, stigmatic bulb; StSc, spiracular scar; StT, stigmatic tube; Tr, trabecula; TP, thoracic papilla; VC, ventral cornu; WP, wing process of hypostomal sclerite.

LIFE HISTORIES

Chlorops obscuricornis Loew

This species is strictly Nearctic in distribution, ranging from Virginia and New York west to Manitoba and Oregon and south to Florida and California (Sabrosky, 1965). Valley et al. (1969) reported that the larvae were primary invaders of stems of *Eleocharis smallii*.

Rearings were initiated from numerous adults and immature stages collected from stands of *E. smallii*, a perennial species having sizeable reddish or purplish rhizomes. The fidelity of *C. obscuricornis* to its host plant was shown by Todd and Foote (1987) who found adults almost exclusively in a stand of *E. smallii*. At another marsh, a few adults were swept from a stand of *E. obtusa* (Willd.) Schultes, an annual species. Numerous adults were also swept from another perennial species, *E. rostellata* Torrey, in a calcareous fen. The flight period, as determined by weekly sweep samples of a stand of *E. smallii* occurring in a roadside ditch, lasted from early June to mid-July (Fig. 54). Adults were most abundant in mid-June.

Laboratory-reared females lived 12–19 days ($n = 8$); males, 8–11 days ($n = 8$). No courtship displays were noted, and it appeared that males merely assaulted any nearby fly of proper size and configuration. Nonreceptive females dislodged males by vigorous kicking of their hind legs. During copulation the male situated himself above the female, facing in the same direction. The fore tarsi rested on the bases of her folded wings, his middle tarsi were applied to the lateral surface of her abdomen, and the hind tarsi grasped the female's genitalic segments.

Both field-collected and reared females laid eggs readily on lengths of *Eleocharis* stems in the breeding jars. All field-collected eggs were found near the bases of stems. The incubation period lasted 5–7 days ($n = 12$). No larvae were reared to the pupal stage in the laboratory-initiated rearings. Second-instar larvae were found during late March feeding as primary invaders in stems of *E. smallii*. A few larvae occurred in young shoots, but most were in larger, older stems. Fully grown larvae were found by the middle of April. Shortly before forming puparia, larvae retreated to the crown, tunneled into one of the rhizomes, reversed direction, and inserted their posterior spiracles into the hollowed-out portion of the rhizome. Field-collected puparia produced adults in 10–15 days under laboratory conditions ($n = 4$).

The abbreviated flight period (Fig. 54) suggests that *C. obscuricornis* is univoltine in northern Ohio. Overwintering apparently occurred as young larvae in quiescence. Larvae collected during the winter months became active in the laboratory and began feeding on *Eleocharis* stem tissue. Larval feeding was completed in nature in April and early May, pupation occurred in late May, and adults emerged in June. Eggs were deposited between mid-June and early July. Larvae fed in the stems until late October.

Diplotoxa inclinata Becker

Diplotoxa inclinata has a transcontinental distribution, ranging from Québec to California and south to New Jersey and Texas (Sabrosky, 1965). It was abundant

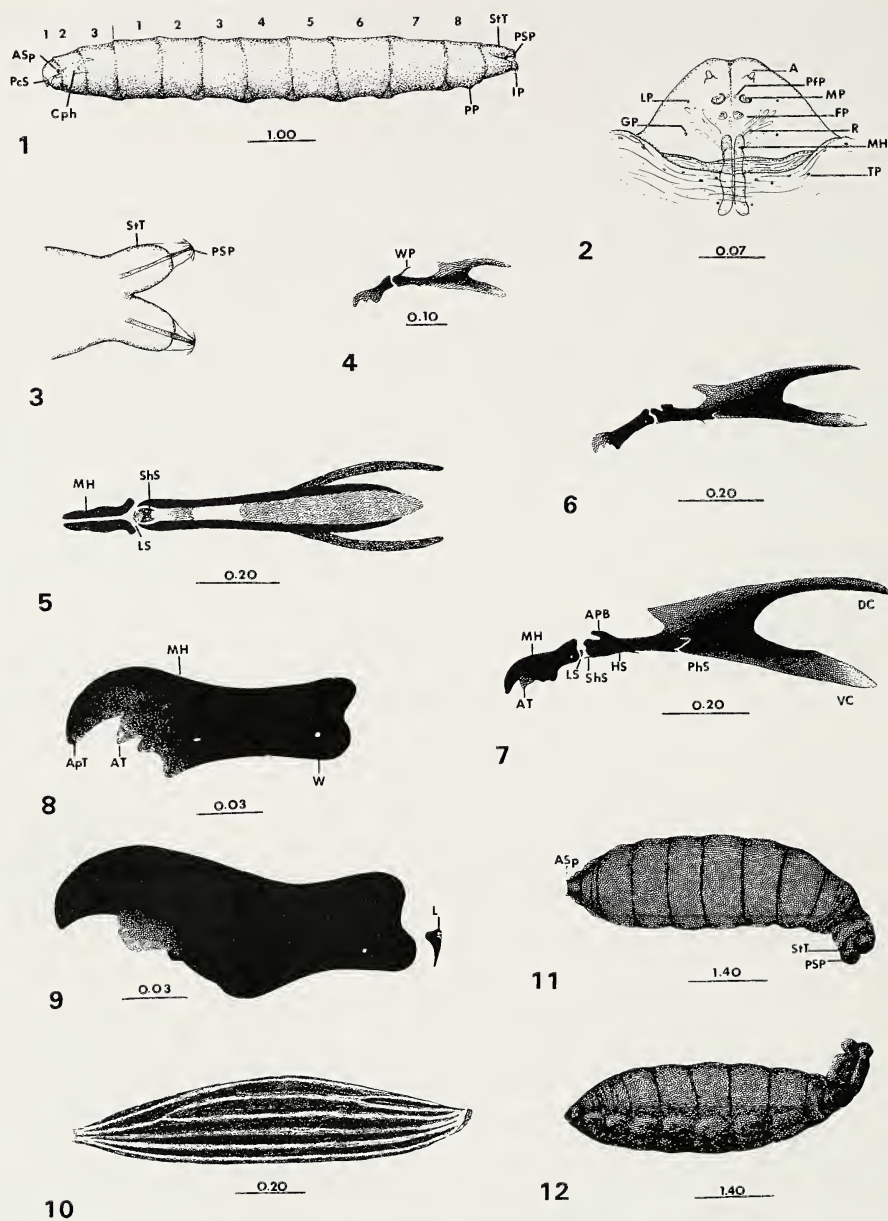


Fig. 1-12.—*Diplotoxa nigripes*. 1. Lateral habitus of larva, third instar. 2. Ventral view of anterior end, same. 3. Dorsal view of posterior end, same. 4. Lateral view of cephalopharyngeal skeleton, first instar. 5. Ventral view of cephalopharyngeal skeleton, third instar. 6. Lateral view of cephalopharyngeal skeleton, second instar. 7. Same, third instar. 8. Mandible, second instar. 9. Same, third instar. 10. Egg. 11. Puparium, dorsal view. 12. Same, lateral view.

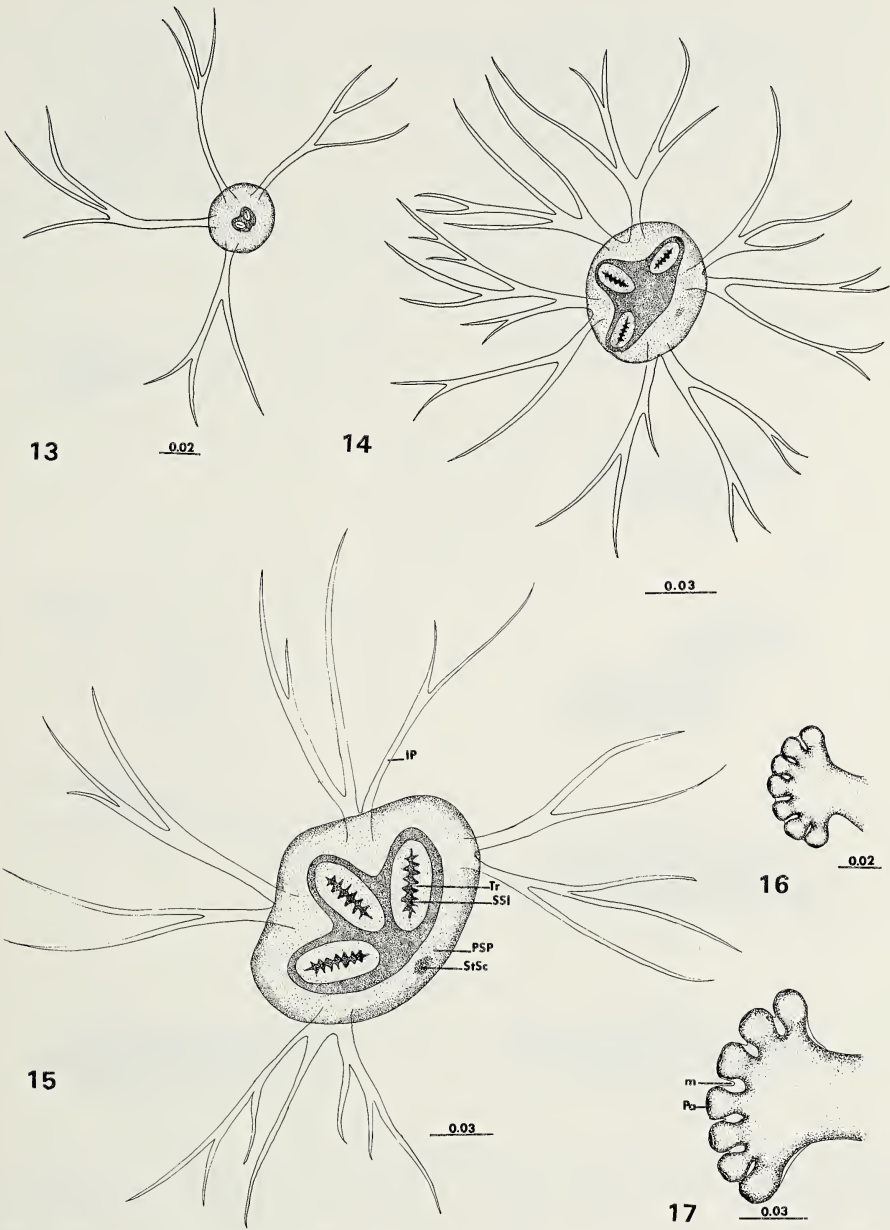


Fig. 13–17.—*Diplotoxa nigripes*. 13. Posterior spiracular plate, first instar. 14. Same, second instar. 15. Same, third instar. 16. Anterior spiracle, second instar. 17. Same, third instar.

in freshwater marshes in northeastern Ohio that contained stands of its host plant, *Eleocharis smallii* (Todd and Foote, 1987). Several adults were also swept from a small stand of *E. obtusa*. This was one of the first species of *Diplotoxa* to emerge in the Kent area, as six adults were collected as early as May 5. The flight period lasted from early May until early September (Fig. 55). Weekly sweep samples of adults strongly suggest that there are two generations a year in northeastern Ohio.

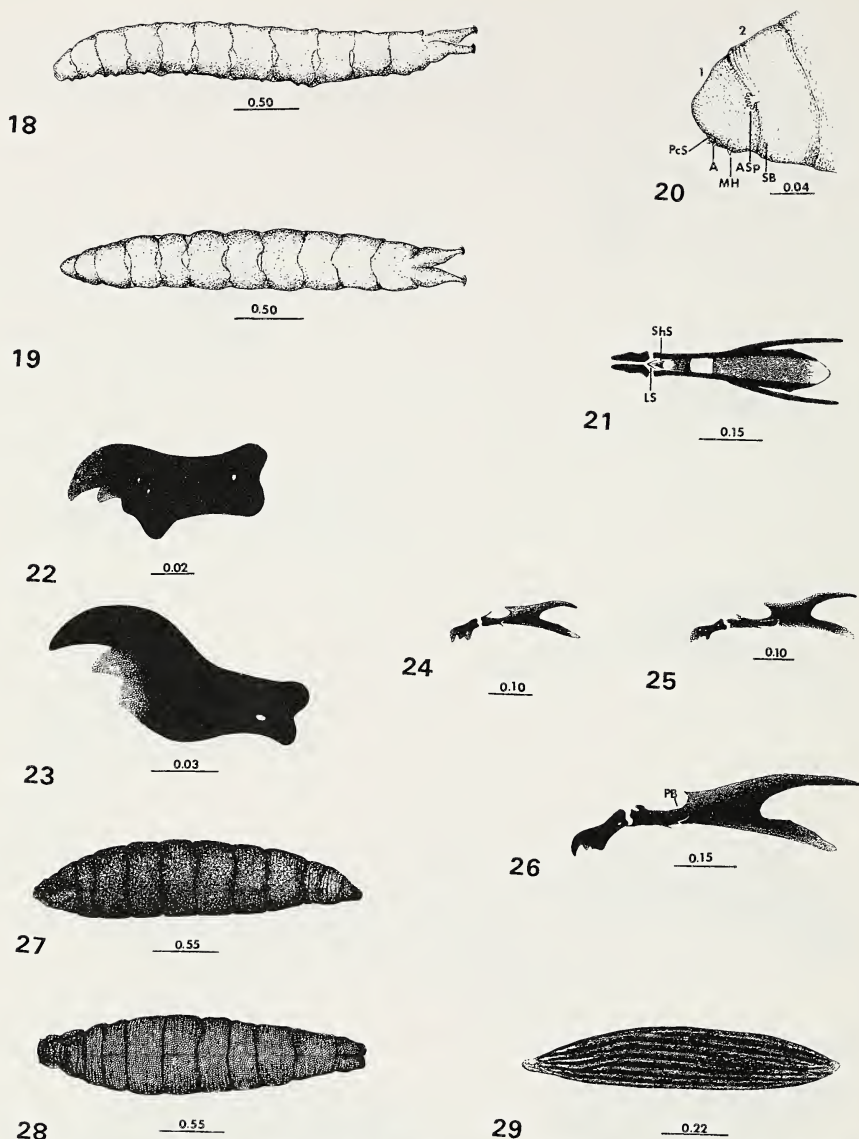


Fig. 18-29.—*Diplotoxa* sp. near *versicolor*. 18. Lateral habitus, third instar. 19. Dorsal habitus, same. 20. Lateral view of segment 1, third instar. 21. Ventral view of cephalopharyngeal skeleton, third instar. 22. Mandible, second instar. 23. Same, third instar. 24. Lateral view of cephalopharyngeal skeleton, first instar. 25. Same, second instar. 26. Same, third instar. 27. Puparium, lateral view. 28. Same, dorsal view. 29. Egg.

Adults usually rested head downward on *Eleocharis* stems. Paired adults placed in breeding jars with lengths of *Eleocharis* spent most of their time on the stems and did not wander freely about the enclosure. Field-collected females lived 7-21 days in the laboratory ($n = 10$); males, 12-17 days ($n = 10$). In contrast, reared females lived only 4-18 days ($n = 5$). Reared females usually had a premating period that lasted less than 24 hr, and one female mated approximately six hours

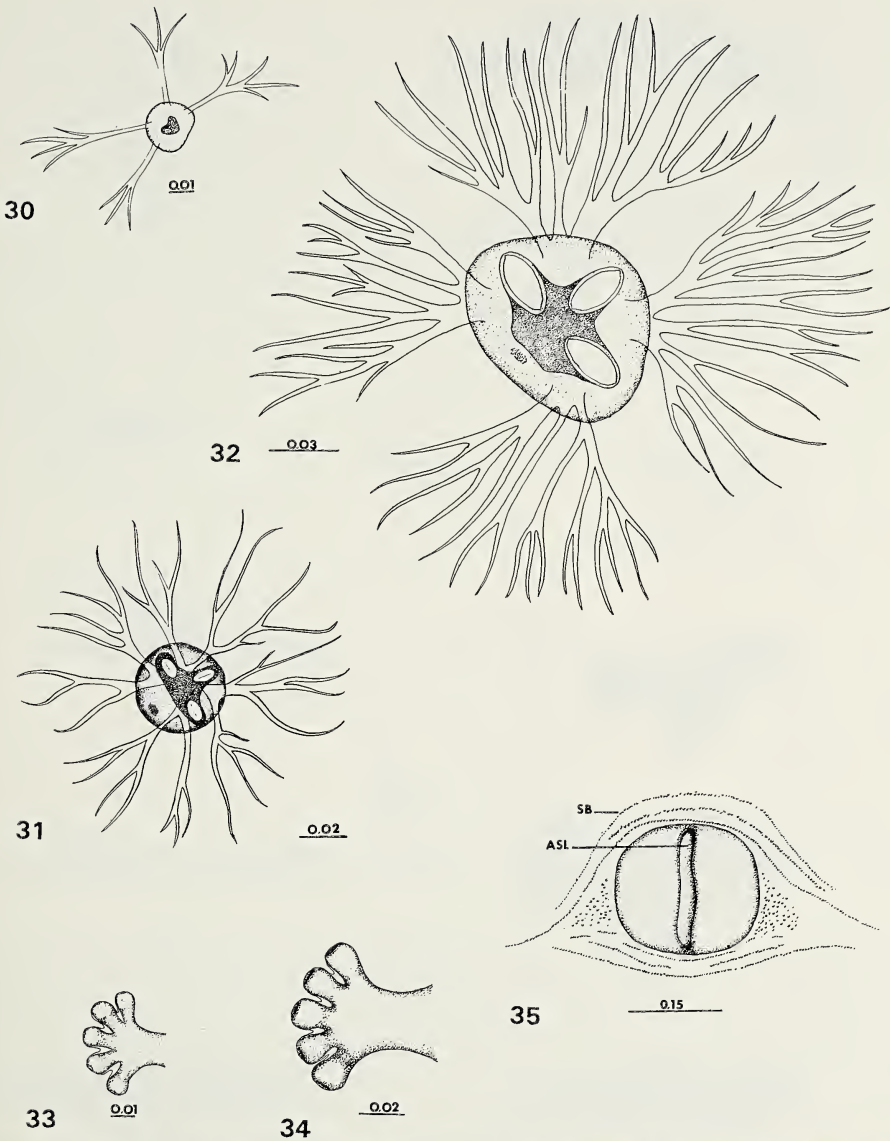


Fig. 30–35.—*Diplotoxa* sp. near *versicolor*. 30. Posterior spiracular plate, first instar. 31. Same, second instar. 32. Same, third instar. 33. Anterior spiracle, second instar. 34. Same, third instar. 35. Perianal pad, third instar.

after emerging. No overt courtship behavior was observed. Mating usually occurred during late afternoon. During coitus, the male positioned himself above the female at about a 45° angle to her body. The head was positioned directly above the anterior portion of her scutellum, the front tarsi rested slightly in front of the wing bases of the female, and the mid and hind tarsi clasped the sides of the female's abdomen. The wings of both sexes remained folded during mating which lasted from eight to over 30 minutes ($n = 12$).

The preoviposition period from mating to the first deposition of eggs usually

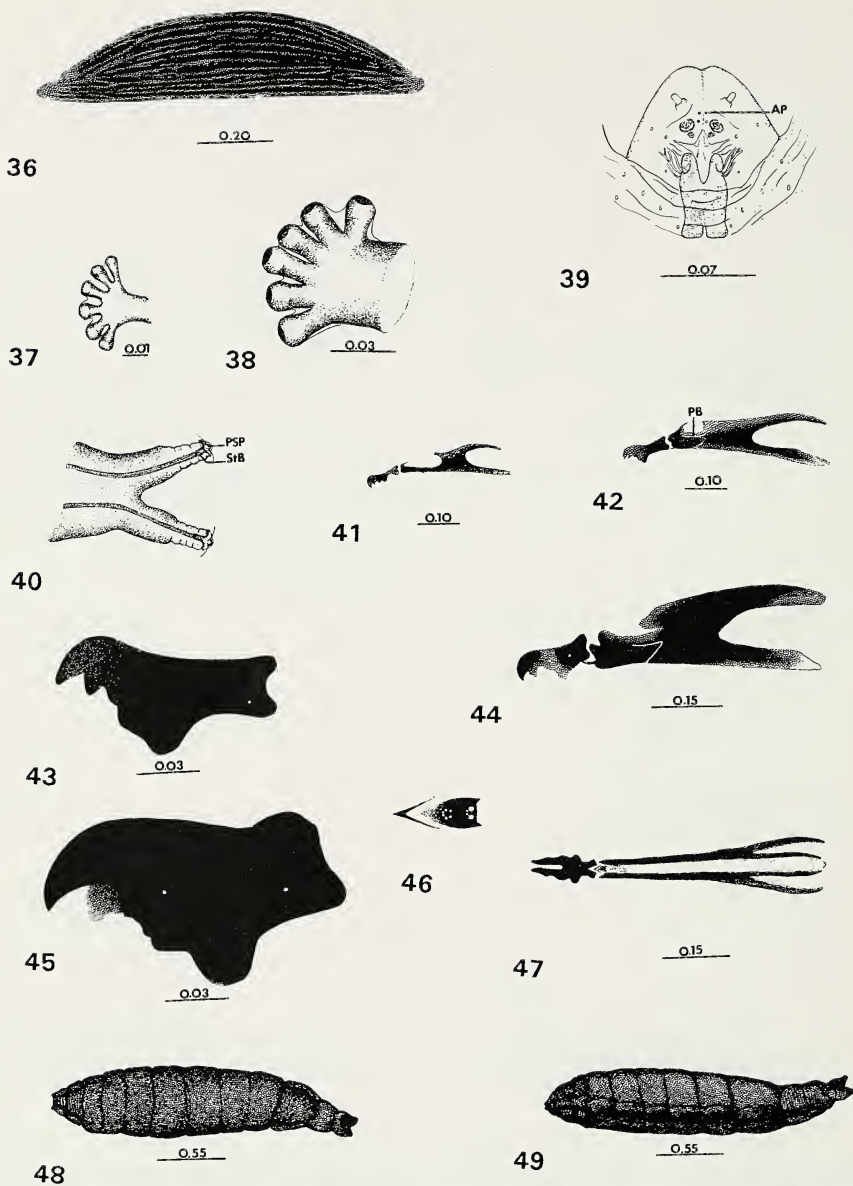


Fig. 36-49.—*Diplotoxa inclinata*. 36. Egg. 37. Anterior spiracle, second instar. 38. Same, third instar. 39. Ventral view of segment 1, third instar. 40. Dorsal view of stigmatic tubes, third instar. 41. Lateral view of cephalopharyngeal skeleton, first instar. 42. Same, second instar. 43. Mandible, second instar. 44. Lateral view of cephalopharyngeal skeleton, third instar. 45. Mandible, third instar. 46. Ventral view of subhypopharyngeal and ligulate sclerites, third instar. 47. Ventral view of cephalopharyngeal skeleton, third instar. 48. Puparium, dorsal view. 49. Same, lateral view.

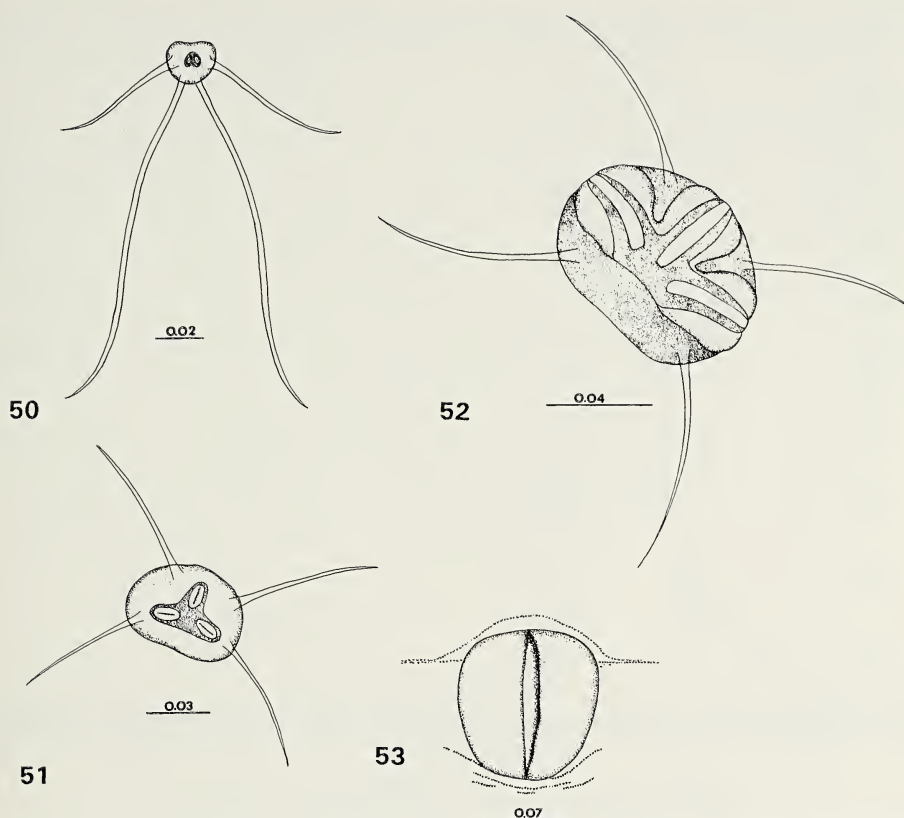


Fig. 50–53.—*Diplotoxa inclinata*. 50. Posterior spiracular plate, first instar. 51. Same, second instar. 52. Same, third instar. 53. Perianal pad, third instar.

was less than a day, and one female began ovipositing six hours after mating. If *Eleocharis* stems were not available, females delayed oviposition for over a week then laid a few eggs on the peat moss that formed a moist substrate in the breeding jars. These females died a day or so after oviposition. In contrast, females confined with *Eleocharis* readily oviposited on the stems and lived for several days after ovipositing. Five females laid 86, 89, 72, 62, and 86 eggs, respectively ($\bar{x} = 79$), over a 16-day period. Usually 4–5 eggs were laid by a female each day once oviposition began. Most of the eggs were deposited at the base of a stem just above the level of the peat moss substrate. A few eggs were placed higher on the stems, but none was placed on the inflorescence. The incubation period lasted 4–5 days ($n = 25$).

In nature, eggs were attached to stems just above the water level and oriented parallel to the stem. One or two eggs were usually found on each stem, although a few stems supported as many as five eggs. Stems occurring in deeper water were more heavily infested than those in shoreline situations.

Newly-hatched larvae crawled down the stem and entered young shoots at the base of the plant where they fed as primary invaders. Following the first larval molt, larvae ate their way downward to the bases of the shoots and penetrated into the rhizomes attached to the crown. Here, they fed on succulent meristematic

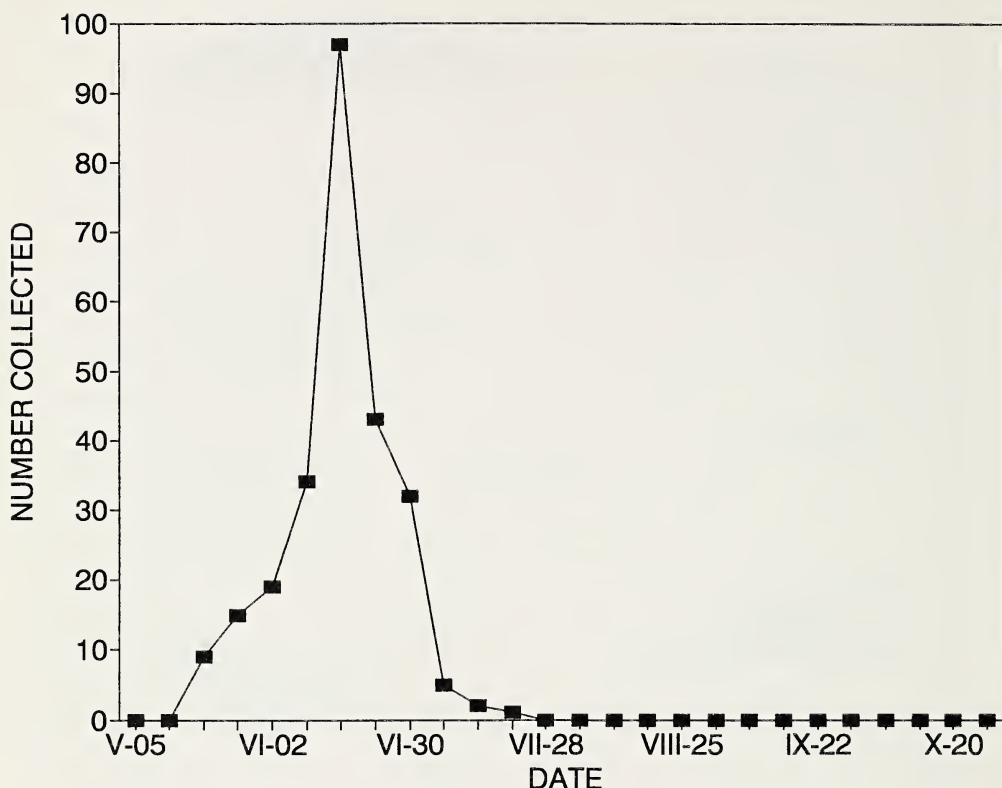


Fig. 54.—Seasonal distribution of *Chlorops obscuricornis*.

tissues, leaving a distinct feeding trail through the rhizome. When a larva reached a tiller arising from the rhizome, it entered the upright shoot and consumed its contents. It then returned to the rhizome and fed along it until another tiller was encountered. This process was repeated several times, and the larva usually was fully grown by the time it reached the tip of the rhizome. Pupation occurred within the feeding trail near the distal end of a rhizome. Shortly before forming a puparium, the larva inserted its posterior spiracles into the living tissue adjacent to the feeding trail.

In the laboratory, newly-hatched larvae were placed on the tip of a rhizome, the succulent tissue of which was surrounded by a protective sheath. Larvae quickly removed under the sheath and began to feed on the meristem. However, duration of larval stadia under laboratory conditions could not be determined. Collections of larvae and puparia in nature allowed for estimations of the third larval and pupal stadia. The third stadium lasted 5–6 days ($n = 12$); the prepupal period, 30–48 hr ($n = 5$); and the pupal period, 10–13 days ($n = 4$).

Overwintering occurred as second instars in quiescence, feeding recommenced in April, and pupation occurred in the last two weeks of April.

The third instars and pupae of this species were easily distinguished from those of the other species of *Diplotoxa* by their greenish color.

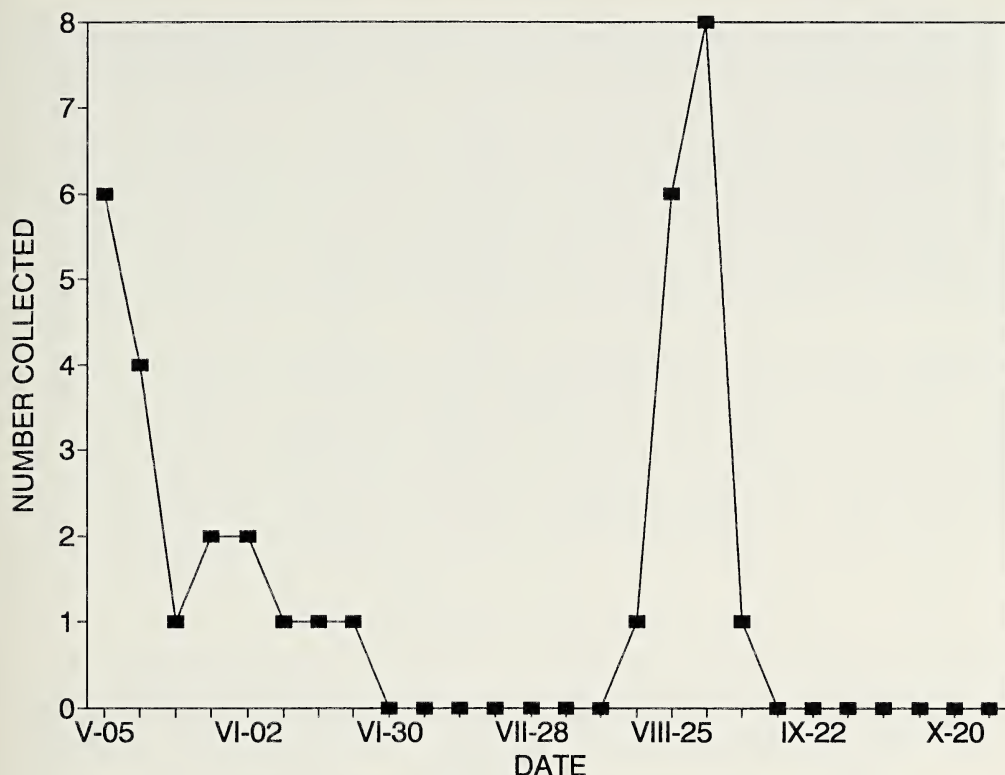


Fig. 55.—Seasonal distribution of *Diplotoxa inclinata*.

Diplotoxa nigripes (Coquillett)

Diplotoxa nigripes ranges from South Dakota and Kansas east to Québec, Maine, and the District of Columbia (Sabrosky, 1965). It was, by far, the most abundant of the three species of *Diplotoxa* collected in Ohio.

Adults were abundant between June 13 and October 3 in strands of *Eleocharis obtusa*, but were only occasionally collected in stands of *E. smallii*. No adults were obtained in the sweep samples taken weekly in a stand of *E. smallii* growing in a roadside ditch, nor in weekly net samples from reed canary grass (*Phalaris arundinacea* L.) and two species of sedges (*Carex lacustris* Willd., *C. stricta* Lam.) in a freshwater marsh near Kent during the warm seasons of 1984 (Todd and Foote, 1987) and 1989. The larval rearings as well as the adult collections indicate that the primary host of this species is *E. obtusa*.

Adults usually rested on the stems of the host plant facing downward. Field-collected males lived 14–37 days in the laboratory ($n = 4$); females, 7–45 days ($n = 8$). In contrast, females reared in the laboratory rarely lived more than 30 days. Mating was observed three times in nature on stems of the host plant during late afternoon. No overt courtship behavior was observed. During copulation, the male was positioned above the female and facing in the same direction with his head at about the level of her scutellum. The wings of both sexes remained folded during mating. The male's fore tarsi rested on the bases of the female's wing, and

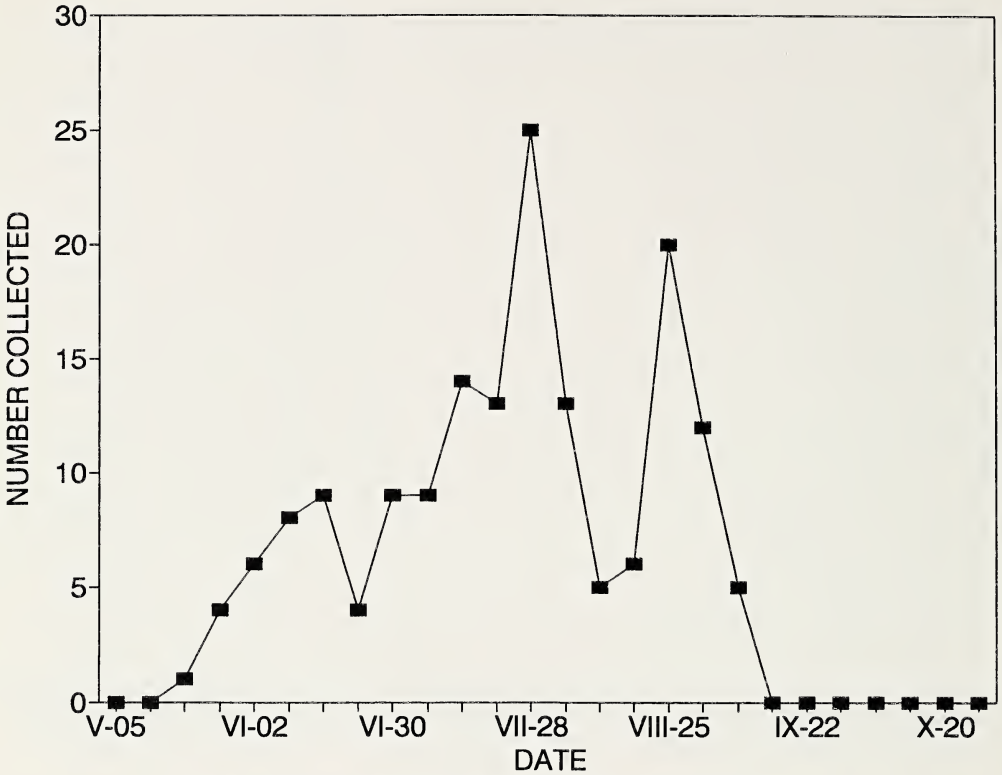


Fig. 56.—Seasonal distribution of *Diplotoxa* sp. near *versicolor*.

the middle and hind tarsi were pressed against the sides of her abdomen. Mating lasted an average of ten minutes ($n = 3$). Males terminated mating by moving anteriorly off the body of the female.

Field-collected females laid numerous eggs in the laboratory breeding jars, although no reared females oviposited. Three females held in the laboratory for 11 days laid 56, 61, and 64 eggs, respectively. Laboratory-held females showed no particular preference for any part of the host plant, although more eggs were deposited on inflorescences and near the base of the stem. In contrast, host plants collected in nature never had eggs anywhere except on the stem bases. Eggs were not inserted into the stem tissue, but were affixed to the upper end of the reddish brown sheath that encircled the lower six inches of the stem. Only one or two eggs were found on each stem.

The incubation period lasted 5–7 days under laboratory conditions, although more than 80% of the eggs laid after the first week of October failed to hatch. The incubation period of those few October-laid eggs that did hatch was considerably extended, lasting 13–15 days. These observations suggest that autumn-deposited eggs enter diapause and overwinter.

The larval stages were very difficult to rear in the laboratory because they would not stay in stems of the host plant once decay commenced, a process that usually began less than a day after the plant was removed from nature. They fed as primary invaders within young shoots, leaving a distinct feeding trail of decaying tissue

as they progressed. Each larva usually attacked at least two shoots, although occasionally as many as five were damaged. Usually only one third instar was found in each plant, although two or more larvae may have initially invaded the plant.

Fully-grown larvae retreated to the base of the shoot in which they had fed and ate a hole into the rhizome to which the shoot was attached. They then reversed position and inserted their relatively long spiracular tubes into the cavity created in the rhizome. This behavior probably ensured an adequate oxygen supply for the developing pupa. The prepupal period from formation of the puparium to appearance of the contained pupa lasted four days; the pupal period, 19–25 days ($n = 5$).

With an incubation period of 5–7 days, a larval period of ca 30 days, a prepupal and pupal period of 23–29 days, and a preoviposition period of at least two or three days, a life cycle was completed in about two months. Overwintering occurred as eggs or as newly-hatched larvae within shoots of the host plant. Larval development accelerated in April, and larvae became fully grown in mid- to late May. Pupation then ensued, and adults emerged during June. Adult numbers increased again in late August, suggesting that two generations a year are produced in northern Ohio.

Diplotaxa sp. near *versicolor* (Loew)

This sibling species of *D. versicolor* was common in northeastern Ohio in freshwater marshes containing its host plants, *Eleocharis obtusa* and *E. smallii*. Numerous adults of *D. versicolor* were swept from a small (3 × 1 m) stand of the path rush, *Juncus tenuis* Willd. (Juncaceae), but were not encountered in stands of *Eleocharis*, suggesting that the two species are trophically separated.

The earliest seasonal record for adults in northeastern Ohio was May 19; the latest, October 8 (Fig. 56). Field-collected females lived 15–47 days in the laboratory ($n = 5$); males, 9–40 days ($n = 7$). Mating behavior and copulation position resembled that of *D. nigripes*.

Laboratory-reared females showed no preference for any particular species of *Eleocharis* and readily oviposited on both *E. obtusa* and *E. smallii* as well as on stems of the rush genus *Juncus*. However, eggs were found only on stems of *E. obtusa* in nature, usually 2.5–5.0 cm above the crown. The incubation period lasted 4–6 days ($n = 15$).

Newly-hatched larvae that were placed near the tips of young shoots of *Eleocharis* quickly crawled down the stem until they encountered the leaf sheath that surrounded the lower half of the stem. They then moved under the edge of the sheath and continued their downward movement to the crown. At the base of the shoot each larva paused and broke into the stem, subsequently feeding as stem borers. Usually only one or two larvae, occasionally three, were found in any one shoot.

Apparently there was only one generation a year in northern Ohio (Fig. 56). Larvae that had fed heavily on young shoots during the summer months remained in the plant tissues as second instars through the ensuing winter. However, overwintering larvae did not appear to be in diapause, as they quickly resumed feeding when brought into the laboratory. Feeding larvae formed a distinct linear trail of browned, decaying tissues as they moved along the length of the shoot.

Fully grown larvae were found near the bases of shoots during late March and early April. Before forming puparia in late April, larvae moved to the base of the

shoots at the crown. Prior to pupating, larvae formed a small cavity in the firm tissue occurring where the shoots united with the roots. The larvae then reversed direction and placed their posterior spiracular tubes in the cavity similar to the behavior observed in *D. nigripes*. The pupal period for the single pupa that produced an adult was 21 days.

Fifteen of the 16 field-collected puparia produced parasitic wasps belonging to an undetermined species of *Chaenusa* (Braconidae).

KEY TO THIRD-INSTAR LARVAE

1. Posterior spiracles at tips of short stigmatic tubes; spiracular plates lacking spiracular hairs *C. obscuricornis*
 Posterior spiracles at tips of very elongate stigmatic tubes (Fig. 3); spiracular plates with spiracular hairs (Fig. 52) 2
2. Spiracular plates appearing trilobed, with unbranched spiracular hairs (Fig. 52); tentoropharyngeal and hypopharyngeal sclerites separate (Fig. 44); living larva usually greenish *D. inclinata*
 Spiracular plates unlobed, with dichotomously branched spiracular hairs (Fig. 32); tentoropharyngeal and hypopharyngeal sclerites partially fused; body of living larva white 3
3. Each spiracular hair with 5-7 branches (Fig. 15) *D. nigripes*
 Each spiracular hair with ten or more branches (Fig. 32)
 *D. sp. nr. versicolor*

DESCRIPTIONS OF IMMATURE STAGES

Diplotoxa inclinata

Egg.—(Fig. 36) length 1.0–1.10 mm, greatest width 0.20–0.25 mm. White, elongate, tapered. Ventral surface very flat, transparent, unridged. Chorion finely striated, with numerous ridges forming a complex pattern. Micropylar end larger than posterior end, both ends smooth and nonstriated.

First-instar Larva.—Similar to third-instar larva except in following characters. Length 1.00–2.80 mm, greatest width 0.20–0.31 mm. White, transparent. Intersegmental constrictions conspicuous. Posterior spiracular plates (Fig. 50) circular, borne at end of elongated stigmatic tubes. Spiracular openings heavily sclerotized, probably two in number. Four unbranched, spiracular hairs, middle two twice as long as remaining two. Cephalopharyngeal skeleton (Fig. 41): length 0.30–0.41 mm; heavily pigmented, posterior portion of tentoropharyngeal cornua hyaline; hypopharyngeal and tentoropharyngeal sclerites fused; no parastomal bars; thin sclerotized wing projecting dorsoposteriorly from hypopharyngeal sclerite; mandibles with two accessory teeth.

Second-instar Larva.—Similar to third-instar larva except in following characters. Length 3.50–4.70 mm, greatest width 0.40–0.60 mm. Posterior spiracular plate (Fig. 51) circular with three heavily sclerotized and indistinct spiracular openings. Four unbranched spiracular hairs, all hairs equal in length. Stigmatic scar and spiracular trabeculae, indistinct. Anterior spiracles (Fig. 37) enclosed in transparent, ensheathing membrane; spiracles creamy white, fan-shaped, with six marginal papillae. Cephalopharyngeal skeleton (Fig. 42) more pigmented than that of first instar. Posterior third of ventral cornua not pigmented. Hypopharyngeal and tentoropharyngeal sclerites almost entirely fused, leaving only faint tract of fusion line between sclerites. Indication of fusion between parastomal bar

and hypopharyngeal sclerites. Remnant of sclerotized wing extending dorsoposteriorly from anterior ridge of hypopharyngeal sclerite, mandibles (Fig. 43) fused dorsally, strongly pigmented except for apical and accessory teeth. One large apical tooth, one and possibly two smaller accessory teeth. Only one window visible.

Third-instar Larva.—Length 5.60–7.50 mm, greatest width 0.60–0.85 mm. Similar to third-instar larva of *D. nigripes* except for following characters. First segment (Fig. 39) bilobed apically, each lobe bearing one short, fleshy two-segmented antenna and one maxillary palp with slightly sclerotized C-shaped ring basally and containing 11–13 papillae. Each lobe also bearing eight sensory papillae, one dorsal and one frontal papilla, three submaxillary papillae (two anterior and one posterior), two lateral papillae, and one genal papilla. Genal rami leading into mouth cavity. Facial mask with numerous, large, posteriorly pointed, V-shaped spinules. Segments 2 and 3 with 10–15 irregular rows of fine spinules, only 5–10 of these rows completely encircling segment. Segments 4–11 with 15–25 overlapping, irregular rows of large, blunt spinules, only 10–15 of these rows continue around segment. Perianal pad (Fig. 53) level with ventral surface; surrounded anteriorly by compact rim of unequal-sized, irregularly-spaced, round spinules and ventrally by three distinct rows of small rounded spinules.

Anterior spiracles (Fig. 38) large and conspicuous, creamy white, extending perpendicularly from body, fan-shaped, with six finger-like marginal papillae, each papilla enclosed within ensheathing membrane. Stigmatic tubes (Fig. 40) elongate, constricted. Posterior spiracular plates (Fig. 52) posterodorsally at apices of stigmatic tubes. Spiracular bulb and spiracular trunk creamy white, large, conspicuous, and trifurcating into three large lobed structures (Fig. 40), each lobe possessing dorsal spiracular opening. Spiracular trunk heavily pigmented, spiracular openings indistinct, appearing as continuous, dark, trilobed structure. Stigmatic scar somewhat circular, not conspicuous. Four unbranched spiracular hairs. Trabeculae indistinguishable.

Cephalopharyngeal skeleton (Fig. 44) length 0.64–0.78 mm. Heavily sclerotized except for posterior ends of dorsal and ventral cornua. Hypopharyngeal and tentoropharyngeal sclerites separate. Parastomal bars present, fused anteriorly to dorsal surface of hypopharyngeal sclerite. Hypopharyngeal sclerite H-shaped in ventral view (Fig. 47). Dorsal cornua of tentoropharyngeal sclerite not joined by bridge; floor of tentoropharyngeal sclerite faintly pigmented. Mandibles (Fig. 45) heavily pigmented except for accessory tooth, fused dorsally, two circular windows, accessory tooth with protrusion anteriorly.

Diplotoxa nigripes

Egg.—(Fig. 10) length 1.15–1.80 mm, greatest width 0.20–0.25 mm. White. Elongate, with micropylar end only slightly larger than posterior end, micropyle turned upward. Ventral surface somewhat flat, opaque with one or two faint ridges. Chorion with 11–12 large, prominent reticulations; micropylar and opposite end without reticulations. Eggs with 4–5 diverging reticulations, one diverging towards posterior end on dorsal surface, remainder on lateral surface.

First-instar Larva.—Similar to third instar except in following characters. Length 1.20–2.18 mm, greatest width 0.20–0.43 mm. White, integument transparent. Posterior spiracular plates (Fig. 13) borne at distal end of elongated stigmatic tubes. Spiracular tubes pigmented, spiracular openings indistinct, but probably two in number, radiating out from stigmatic scar. Four spiracular hairs, each with one main trunk bifurcating at distal end. Metapneustic. Cephalopharyngeal skel-

eton (Fig. 4) pigmented except on posterior portion of ventral cornua and tip of dorsal cornua, length 0.35–0.50 mm. Hypopharyngeal and tentoropharyngeal sclerites fused, no parastomal bars. Thin sclerotized wing projecting dorsoposteriorly from dorsoanterior ridge of hypopharyngeal sclerite. Mandibles of one sclerite, one accessory tooth.

Second-instar Larva.—Similar to third instar except in following characters. Length 2.40–3.81 mm, greatest width 0.55–0.68 mm. Posterior spiracular plate (Fig. 14) circular to oval, three sclerotized and indistinct spiracular openings appearing as dark, trilobed structure. Four branched spiracular hairs. Stigmatic scar not distinct. Trabeculae indistinct. Anterior spiracles (Fig. 16) creamy white, fan-shaped, with seven marginal papillae. Transparent membrane enclosing papillae. Cephalopharyngeal skeleton (Fig. 6) pigmented except on posterior end of ventral cornua. Length 0.58–0.68 mm. Hypopharyngeal and tentoropharyngeal sclerites showing fusion line. Most of each parastomal bar fused with dorsal surface of hypopharyngeal sclerite. Anterior end of bar forming knob-like protuberance anterodorsally from hypopharyngeal sclerite. Mandibles (Fig. 8) well-pigmented except for apical and accessory teeth, one sclerite; one large apical tooth and two accessory teeth. Subhypostomal and ligulate sclerites semitransparent.

Third-instar Larva.—(Fig. 1) length 5.50–6.70 mm, greatest width 0.85–1.00 mm. Creamy white, integument transparent to translucent. Body elongate, cylindrical, tapering anteriorly from third thoracic segment. Posterior end tapering and terminating in two elongated stigmatic tubes. Body of stigmatic tube (Fig. 3) thick, integument extending beyond body, terminating in spiracular plates. First segment (Fig. 2) bilobed apically, each lobe bearing short, two-segmented antenna, two maxillary palps, each palp with slightly sclerotized basal C-shaped ring, six maxillary papillae; six sensory papillae including one prefrontal, three frontal (two anterior, one posterior), one or two lateral, one genal papillae. Genal rami thin, not bifurcating, directed toward oral opening. Facial mask with numerous rows of spinules that completely encircle larva.

Spinule bands with 20–30 short, irregular rows of spinules at anterior end of all thoracic and abdominal segments. Spinules in abdominal segments reduced and indistinct, forming a fine, linear fold. Spinule bands more numerous on ventral surface, only 10–15 rows continuing around segment.

Anterior spiracles (Fig. 17) large, conspicuous, perpendicular to body. Creamy white, fan-shaped with seven finger-like marginal papillae, ensheathing membrane extending closely over papillae.

Posterior spiracular plates (Fig. 15) circular, located distally on stigmatic tubes. Spiracular bulb and spiracular trunk not conspicuously enlarged or trifurcating (Fig. 3). Three spiracular openings not distinct, appear as continuous, dark, trilobed structure. Stigmatic scar present but not conspicuous. Four spiracular hairs, each immediately bifurcating into two main branches and many secondary branches. Trabeculae approximately 18 per spiracular opening.

Cephalopharyngeal skeleton (Fig. 7) length 0.88–0.95 mm. Heavily sclerotized except transparent posterior ends of dorsal and ventral cornua. Hypopharyngeal and tentoropharyngeal sclerites not completely fused. Parastomal bar fused with dorsal surface of hypopharyngeal sclerite, anterior end of parastomal bar extending anterodorsally from hypopharyngeal sclerite. Dorsal cornua not joined by bridge, floor of tentoropharyngeal sclerite lightly pigmented. Floor of hypopharyngeal sclerite (Fig. 5) wide, lightly sclerotized, H-shaped when viewed ventrally. Mandibles (Fig. 9) heavily pigmented except for accessory tooth, one posterior window.

Not connected dorsally, large apical tooth, one blunt accessory tooth. Subhypostomal sclerite beneath anterior edge of hypopharyngeal sclerite, with two large circular windows, slightly visible when viewed internally. Ligulate sclerite semi-transparent, V-shaped, anterior to subhypostomal sclerite, anvil shaped when viewed laterally.

Puparium.—(Fig. 11, 12) length 5.10 mm, greatest width 1.50 mm. Mostly light golden-brown, dark brown to black anteriorly, stigmatic tubes black. Cuticle very thin and transparent, developing pupa clearly visible. Elongated anterior and posterior ends dorsoventrally flattened to form distinct lateral ridges on segments 1–4 and 9–11. Stigmatic tubes large, heavily sclerotized, extending in various positions. Anterior spiracles poorly developed, located anteriorly on dorsal cephalic cap, fan-shaped and silver-white, with seven marginal papillae. Posterior spiracular plate rounded, spiracular openings indistinct. Perianal pad depressed. Puparium retaining spinule bands of third-instar larva.

Diplotoxa sp. near *versicolor*

Egg.—(Fig. 29) length 0.80–1.00 mm, greatest width 0.12–0.15 mm. White, elongate, and tapered. Ventral surface somewhat flattened, transparent and unridged. Chorion striated, with ridges diverging and converging especially at ends and on the dorsal surface. Micropylar end larger than posterior end, both ends smooth and nonstriated.

First-instar Larva.—Similar to third instar except in following characters. Length 0.90–2.20 mm, greatest width 0.15–0.21 mm. White, integument transparent. Posterior spiracular plates (Fig. 30) at ends of elongated stigmatic tubes. Spiracular trunks deeply pigmented. Spiracular openings not distinguishable, probably two in number positioned to form dark, heart-shaped structure. Four spiracular hairs, each with single long trunk terminating in either three or four shorter branches. Larva metapneustic. Cephalopharyngeal skeleton (Fig. 24) length 0.25–0.35 mm, pigmented except for hyaline posterior portion of ventral cornua and tip of dorsal cornua. Hypopharyngeal and tentoropharyngeal sclerites fused, parastomal bars lacking. Thin, sclerotized wing projecting dorsoposteriorly from dorsoanterior ridge of hypopharyngeal sclerite. Mandibles with one accessory tooth.

Second-instar Larva.—Similar to the third instar except in following characters. Length 3.20–4.00 mm, maximum width 0.45–0.60 mm. Posterior spiracular plate (Fig. 31), circular to oval, three indistinct spiracular openings on brown, trilobed structure. Four, multibranched spiracular hairs, each with short trunk that forks into two main branches that each terminate in 2–6 shorter branches. Stigmatic scar and trabeculae indistinct. Anterior spiracles (Fig. 33) creamy white, fan-shaped, with five marginal papillae; with transparent ensheathing membrane around papillae. Cephalopharyngeal skeleton (Fig. 25) more pigmented than in first instar. Posterior ends of ventral cornua not pigmented. Hypopharyngeal and tentoropharyngeal sclerites almost entirely fused. No dorsal wing extending from hypopharyngeal sclerite. Parastomal bars fused to hypostomal sclerite except for anterior end which appears as thick, anterodorsal protuberance. Mandibles well-pigmented except for apical and accessory teeth; one large apical tooth and two accessory teeth; 4–6 circular windows. Subhypostomal and ligulate sclerites poorly pigmented.

Third-instar Larva.—(Fig. 18, 19) similar to third-instar larva of *D. nigripes* except in following characters. Length 4.50–5.50 mm, maximum width 0.70–0.95 mm. Maxillary palp of segment 1 (Fig. 20) with 7–11 papillae. Facial mask with

numerous large, V-shaped spinules. Segment 1 with 20–25 compact, short, irregular rows of spinules at anterior end, spinule rows completely encircling segment. Segments 2 and 3 with 15–20 thick, irregular rows of large, blunt spinules that encircle anterior end of each segment. Spinule bands dark due to slight sclerotization or impregnation by dirt. Segments 4–8 with 15–20 short, irregular rows of V-shaped spinules encircling segments. Spinule bands on dorsal surface more linear, fine, and composed of smaller spinules. Ventral surface of segments 9 and 10 containing approximately 20–30 short, irregular, fine rows of spinules, only 7–15 rows encircling segments. Segment 11 with reduced spinule bands, individual spinules indistinct, forming fine lines, no spinule bands on dorsal surface. Perianal pad (Fig. 35) with three fine rows of spinules anteriorly and 3–5 rows posteriorly, cluster of irregularly spaced large, U-shaped spinules between anterior and posterior rows.

Anterior spiracles (Fig. 34) large, conspicuous, creamy white, extending perpendicularly from body, fan-shaped, with five finger-like marginal papillae, each papilla enclosed within ensheathing membrane. Stigmatic tubes elongate. Posterior spiracular plates (Fig. 32) posterodorsally at end of stigmatic tubes. Stigmatic bulbs and spiracular trunks normal. Spiracular trunks heavily pigmented, spiracular openings indistinct, appearing as continuous, dark, trilobed structure. Stigmatic scar somewhat ovoid. Four, multibranched spiracular hairs, each with main trunk diverging into three or four branches that terminate in many smaller branches. Trabeculae indistinguishable.

Cephalopharyngeal skeleton (Fig. 26) length 0.70–0.90 mm, greatest width 0.15 mm. Heavily sclerotized except for posterior end of ventral cornua. Hypopharyngeal and tentoropharyngeal sclerites partially fused. Parastomal bars fused with dorsal surface of hypopharyngeal sclerite, anterior end of parastomal bar extending out anterodorsally from hypopharyngeal sclerite. Hypopharyngeal sclerite H-shaped when viewed ventrally (Fig. 21). Floor of tentoropharyngeal sclerite (Fig. 21) lightly pigmented except for transparent posterior end, dorsal cornua not joined by bridge. Mandibles (Fig. 23) heavily pigmented except for accessory tooth, one circular window. Subhypostomal sclerite beneath anterior edge of hypopharyngeal sclerite, somewhat heart-shaped. Slightly visible when viewed laterally, ligulate sclerite V-shaped, elongate, anterior of subhypostomal sclerite, semitransparent. No dentate sclerites.

Puparium. —(Fig. 27, 28) similar to puparium of *D. nigripes* except in following characters. Length 2.80–3.30 mm, greatest width 0.75–0.90 mm. Gold to reddish brown, dark brown cephalic cap. Cuticle slightly transparent. Anterior spiracles poorly developed, anterior on dorsal cephalic cap, fan-shaped with five marginal papillae. Spinule bands appearing ridge-like, completely encircling segments, becoming coarse and deeply grooved at anterior and posterior ends of puparium. Intersegmental constrictions distinct. Segment 1 partially invaginated. Posterior stigmatic tubes flattened dorsoventrally, deeply pigmented posteriorly. Spiracular plates black, oblong, spiracular openings not visible. Anal slit distinct, slightly depressed.

DISCUSSION

This study suggests that the larval stages of many, if not all, species of the genus *Diploptoxa* are associated with spike-rushes of the genus *Eleocharis*. Adults of seven species were collected in Ohio or Montana from stands of *Eleocharis* (Wearsch, 1968), eggs of at least five species were discovered on *Eleocharis* stems, and larvae of four species were found feeding in stems or rhizomes.

Eleocharis plants are infrequently attacked by other insect larvae except for a few species of Lepidoptera and Coleoptera. *Eleocharis* species grow in marshy areas, along with other sedges and rushes, frequently form extensive pure stands, and are relatively undisturbed by human activity. The many sprouts, which are continually produced at the base of the plant during the warm season, and the thick, branched rhizome system offer very succulent food sources. Meristematic tissue in monocots such as *Eleocharis* is basal in position within the stem, and typically has a higher energy content than nonmeristematic tissue (Hirose et al., 1989), which explains the concentration of feeding by chloropid larvae at the base of the stem or in rhizomes.

Primary invaders (larvae feed on living plant tissue) of *Eleocharis* stems are best represented by *C. obscuricornis*, *D. sp. near versicolor*, and *D. nigripes*. In contrast, the morphology of the larvae of *D. inclinata* includes some features of a secondary invader (larva feeds on tissue damaged by a primary invader) and some of a primary invader. A comparison of the cephalopharyngeal skeleton of various species of primary and secondary invaders in the family Chloropidae indicates that secondary invaders possess separate tentoropharyngeal and hypopharyngeal sclerites, whereas these sclerites are fused in primary invaders.

Although the overall appearance of chloropid larvae is similar, species are distinguishable in size, color, and appearance of the stigmatic tubes and spiracular hairs. *Chlorops* larvae differ from those of *Diplotoxa* in having spiracular openings at the distal ends of sclerotized extensions that protrude from short stigmatic tubes, and in lacking spiracular hairs. In contrast, larvae of *Diplotoxa* possess very elongate stigmatic tubes and have long spiracular hairs.

Identifying species of *Diplotoxa* from preserved larval specimens is difficult, although living larvae of *D. inclinata* are easily distinguished from those of the other species we studied by their greenish color. The bulb and internal stigmatic chamber of the stigmatic tubes of this species are enlarged, have a dark creamy color, and branch into three prominent lobes. The spiracular plate possesses a trilobed structure bearing the spiracular slits and has only four nonbranching spiracular hairs. *Diplotoxa sp. near versicolor* and *D. nigripes* have semitransparent internal stigmatic chambers, with the spiracular slits opening onto the flat spiracular plate. Both have a complex network of spiracular hairs.

The anterior spiracles of all three species of *Diplotoxa* consist of a fan-shaped structure with apical papillae. The number of papillae is relatively constant and distinctive for each species. *Diplotoxa sp. near versicolor*, the smallest of the three species, possesses five papillae; *D. inclinata*, the next largest, has six; and *D. nigripes*, the largest, has seven.

The cephalopharyngeal skeletons of *D. sp. near versicolor* and *D. nigripes* differ in only a few structures, whereas both differ markedly from that of *D. inclinata*. The skeletons of the first-instar larvae of *D. nigripes* and *D. sp. near versicolor* are almost identical, having a wing projecting from the anterior end of the hypopharyngeal sclerite, but the skeleton of *D. nigripes* is much larger. In the second instar of both species the wing of the hypopharyngeal sclerite is reduced or absent, and a knob-like structure is present. This knob probably is the anterior portion of the parastomal bar, the remainder of which has fused with the dorsal surface of the hypopharyngeal sclerite. The hypopharyngeal and tentoropharyngeal sclerites are not completely fused in the third instars of both species, suggesting that larvae of these species originally fed as secondary invaders of damaged stems. Fusion of these two sclerites probably gives greater support and rigidity to the cephalopharyngeal skeleton.

Diplotoxa inclinata apparently became a primary invader very recently, as the tentoropharyngeal and hypopharyngeal sclerites in the third instar are still separate. However, the cephalopharyngeal skeleton of the first instar resembles that of *D. sp. near versicolor* and *D. nigripes*. The projecting wing of the hypostomal sclerite is reduced in the second instar, and the parastomal bar, although evident, has fused anteriorly with the base of the projecting wing of the hypopharyngeal sclerite. In the third instar, this fusion is more nearly complete but not to the degree seen in third instars of the other two species. The third instar of *D. inclinata* has the mandibles fused dorsally, which may give greater rigidity for feeding upon the hard tissues of the rhizome.

The shape of the posterior spiracles is helpful in distinguishing among larvae of the four species. Two spiracular openings occur in the first instar, and three in the second and third instars. The spiracles in *D. nigripes* and *D. sp. near versicolor* are similar, although *D. nigripes* is larger, and all three *Diplotoxa* species possess spiracular hairs. The first instar has four large hairs with one or two terminal branches. The hairs of the second instars are more complex: each hair has a main trunk that divides immediately into two large branches, each of which in turn divides two or more times. The third instar possesses a very fine network of four sets of spiracular hairs. The basal trunk of each hair radiates immediately into three or four main branches, each of which branches again to form a fine network. In *D. inclinata*, in contrast, the spiracular hairs of all three instars are reduced and unbranched. The first instar has two very long and two shorter hairs, whereas in the second and third instars the four hairs are equally long.

In *C. obscuricornis* the posterior spiracles are reduced, sclerotized structures with three spiracular slits but no spiracular hairs. Oldroyd (1964) reported that some stem-boring species of *Chlorops* have become so well-adapted to their environment that the posterior spiracles are vestigial. They absorb oxygen through the cuticle. Larvae of *C. obscuricornis* show a tendency toward reduction of the posterior spiracles.

Larvae of all four species, whether feeding on stems or rhizomes, inserted their stigmatic tubes into living tissue or air spaces before forming puparia. This probably is a mechanism for ensuring sufficient oxygen for pupal development. Under natural conditions, pupae in living plants developed normally and produced adults. When cut plants containing puparia were brought into the laboratory, the pupae died shortly after the plants began to decay. Pupae that were removed from stems and placed upon peat moss continued to develop and eventually produced adults.

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BEADS AND PENDANTS FROM TRANTS, MONTSERRAT:
IMPLICATIONS FOR THE PREHISTORIC LAPIDARY
INDUSTRY OF THE CARIBBEAN

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ABSTRACT

Analysis of a collection of lithic beads and pendants from Montserrat suggests that the Trants site may have been a prehistoric lithic bead manufacturing center specializing in carnelian beads. Carnelian is represented in all stages of the manufacturing process. The absence of known local sources for carnelian, the relatively low proportion of finished carnelian beads, the relatively high proportion of broken to unbroken bead "blanks" (indicative of breakage sustained during the manufacturing process), and the relative homogeneity of bead blanks compared to finished beads support the hypothesis of a specialized local manufacturing industry. The presence of a variety of other exotic (nonlocal) materials in finished beads and pendants, including some whose likely sources are in South America, is further evidence of long-distance trading by the early Saladoid residents of Trants. Although the S. W. Howes collection of the Museum of the American Indian, Heye Foundation, was surface-collected, the analysis presented here is consistent with more recent findings of lithic beads from excavated contexts.

INTRODUCTION

The Trants site, further described in Watters (1980) and Petersen and Watters (1991), is located on the windward (east) coast of Montserrat, one of the smaller volcanic islands in the northern Lesser Antilles (Fig. 1). Montserrat is a mountainous island with a total land area of about 98 km². Trants is situated on the only sizeable stretch of relatively flat land on the windward coast. Diagnostic artifacts of the Saladoid ceramic series, including white-on-red painted and zone-incised-crosshatch sherds, are indicative of an early Ceramic Age population movement onto Montserrat. Two early radiocarbon dates from Trants, 2430 ± 80 and 2390 ± 90 B.P. (ca. 480 and 440 B.C. uncorrected), suggest an onset of Saladoid migration into the Lesser Antilles earlier than previously assumed (Petersen and Watters, 1991).

This paper describes a collection of surface-collected lithic beads and pendants from Trants in the Museum of the American Indian. Analysis of this collection, coupled with an analysis of excavated specimens (Bartone and Crock, 1991) suggests that lithic beads may have been manufactured at Trants. Carnelian in particular is amply represented in all stages of bead manufacture. The presence of finished beads and pendants of other nonlocal materials, including some whose likely sources are in South America, is suggestive of long-distance trading by the early Saladoid residents of Trants.

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Submitted 1 November 1993.



Fig. 1.—The Trants prehistoric site is located on the east coast of Montserrat in the northern Lesser Antilles.

THE HOWES COLLECTION

In 1924, the Museum of the American Indian (MAI), Heye Foundation, in New York City, cataloged a collection of some 1073 artifacts from Montserrat. Seymour Wylde Howes (Fig. 2), a recipient of the O.B.E. (Order of the British Empire) for his innovations in agricultural practices, assembled this collection while manager of the Trants Estate (Fig. 3) where he lived until his death in 1927. Queenie Howes van der Veer, Howes' daughter, distinctly remembers her father collecting beads and pieces of pottery from newly-tilled fields (personal communications, 1979–1993). S. W. Howes personally searched whatever field was being worked each day and also encouraged the workers to bring him artifacts they found, for which he paid them a nominal amount. Bruce Howes, S. W. Howes' son, recalls (personal communication, 1993) that the majority of the beads were recovered from Pigeon Field, an area that corresponds for the most part to the fields numbered 1, 2, 3, 8, and 9 by Petersen and Watters (1991:fig. 1).

Queenie van der Veer and Bruce Howes are confident that all of the objects in their father's collection come from the Trants site. Although the possibility exists that workers may have found beads elsewhere and given them to Howes in exchange for the modest reward that he paid them, it is important to note that no lithic beads have been recovered from any other prehistoric site on Montserrat (Watters, 1980).

The arrival of the Howes collection at the MAI created considerable interest. The beads were particularly noteworthy. Harrington (1924) described them in the first published article dealing with artifacts from the Howes collection. Most of the beads were stored at the MAI Research Branch in the Bronx, where our research was conducted in 1985 and 1991. Forty-six beads were on display and were not available for study.

Table 1 lists the 1053 items currently present in the S. W. Howes collection



Fig. 2.—Seymour Wylde Howes, O.B.E., the person who assembled the Howes collection.

according to four general categories: groundstone, shell, pottery, and beads and related artifacts. There are 502 beads and related objects in the Howes collection. Although the MAI has three other collections from Montserrat, the Huckerby collection contains the only other stone bead (catalog number 8/6068), which we also examined. Our study thus includes all lithic beads and related materials from Montserrat available for study at the MAI.

The 503 beads and related artifacts were classed using a scheme based on an object's *substance*, *configuration*, *condition*, and *perforation*. The first classificatory level, *substance*, identifies the composition (Table 2). There are 494 lithic (stone), one ceramic, one shell, and seven glass objects. Only the 494 lithic objects are treated in this paper. The second classificatory level, *configuration*, includes form, shape, and geometry. Artifacts were assigned to one of four basic forms: bead, pendant, blank, and raw material. A relationship between a fifth basic form, "roller" ($n = 4$), and a bead and pendant manufacturing industry could not be established; therefore, these artifacts are not considered here.

There is some ambiguity in the way that the terms "bead" and "pendant" have been employed in popular usage. For the purpose of this study, a "bead" is defined as a single-perforated object that is symmetrical around a longitudinal axis running



Fig. 3.—Trants Estate House as it appeared in the 1920s when Queenie and Bruce Howes lived there as children.

through the center of its perforation. In contrast, a “pendant” is an object that is *not* symmetrical with regard to any of the axes running through any of its perforations. Thus, a pendant’s center of gravity is offset from the perforation through which it presumably was strung, causing it to “hang” or “be suspended” with an inherent orientation (or orientations) relative to its axis (or axes). Figure 4, which is adapted from Durand and Petitjean Roget (1991:68), illustrates the distinction between beads and pendants.

Eleven objects that might be classed as “beads,” in that they are symmetrical around a longitudinal axis running through the center of a perforation, presented

Table 1.—*Expected and observed artifacts.*

Artifact category	Expected quantities* based on catalog cards	Observed quantities			Discrepancy
		Research branch	Exhibit	Total	
Howes Collection					
Groundstone	162	162 ^b	0	162 ^b	0 ^b
Shell	91	90 ^b	1	91 ^b	0 ^b
Pottery	252	246 ^b	6	252 ^b	0 ^b
Beads	551	502 ^c	46	548 ^c	3
Total	1056	1000	53	1053	3
Huckerby Collection					
Beads	1	1 ^c	0	1 ^c	0
Total beads		503 ^d	46	549 ^d	

^a Excludes objects exchanged with University Museum, University of Pennsylvania.
^b Groundstone, shell, and pottery specimens in the Research Branch were not all counted; expected and observed quantities are presumed to be equal; if they are not, discrepancies could pertain.
^c Specimens counted.
^d Howes and Huckerby collections.

Table 2.—Levels of classification for the 503 artifacts studied.

Classificatory level 1 (substance)	Classificatory level 2 (configuration)			Classificatory level 3 (condition)	Classificatory level 4 (perforation)		Category	n
	Form	Shape	Geometry		Number	Stage		
lithic	bead	regular	rounded	intact	1	finished	01	303
lithic	bead	regular	faceted	intact	1	finished	02	12
lithic	bead	regular	rounded	broken	1	finished	03	46
lithic	bead	regular	faceted	broken	1	finished	04	5
lithic	bead	regular	rounded	intact	1	unfinished	05	4
lithic	bead	regular	faceted	intact	1	unfinished	06	1
lithic	bead	regular	rounded	broken	1	unfinished	07	1
lithic	bead	regular	faceted	broken	1	unfinished	08	0
lithic	bead	regular	rounded	intact	2	finished	09	10
lithic	pendant	—	—	intact	—	—	10	10
lithic	bead	regular	rounded	broken	2	finished	11	1
lithic	pendant	—	—	broken	—	—	12	2
lithic	bead	irregular	—	intact	1	finished	13	1
lithic	other	—	—	—	—	—	14	0
lithic	blank	regular	rounded	intact	0	—	15	48
lithic	blank	regular	faceted	intact	0	—	16	0
lithic	blank	regular	rounded	broken	0	—	17	22
lithic	blank	regular	faceted	broken	0	—	18	2
lithic	blank	—	—	intact	0	—	19	2
lithic	raw material	—	—	—	0	—	20	20
ceramic	bead	regular	rounded	intact	1	finished	21	1
shell	bead	regular	rounded	intact	1	finished	22	1
glass	bead	regular	rounded	intact	1	finished	23	4
glass	bead	regular	faceted	intact	1	finished	24	3
lithic	roller	regular	rounded	intact	0	—	25	4
Total								503

a classificatory problem because they have a second perforation, typically transverse and often nearer to one “end” than the other. It is possible that these objects were strung as beads, with the additional perforation used for the insertion of objects such as feathers (cf. Fewkes, 1922:232). These double-perforated artifacts (Fig. 5) were eliminated from the analysis.

For the most part, the beads and pendants are finished products in that the stages of manufacture are complete and the object is ready to be worn. In some cases, however, earlier stages in the manufacturing process are represented by objects designated as “blanks” and “raw materials.” Blanks (Fig. 6), which range from those merely “roughed out” to those lacking only perforation, illustrate numerous stages in the manufacturing process.

Other aspects (shape and geometry) of artifact configuration were adapted from Horace C. Beck’s article on bead classification and nomenclature. Page and figure citations in the present paper refer to the 1981 reprint edition of Beck’s 1928 work. Beck’s (1981) figures 1, 2, and 3 and plates I, II, III, IV, were particularly useful.

Following Beck (1981:4), beads and blanks were classed as regular or irregular. Those with regular shape were then sorted by geometry, as rounded or faceted, and by *condition*, intact or broken. The final classificatory level, *perforation*, has been explained above.

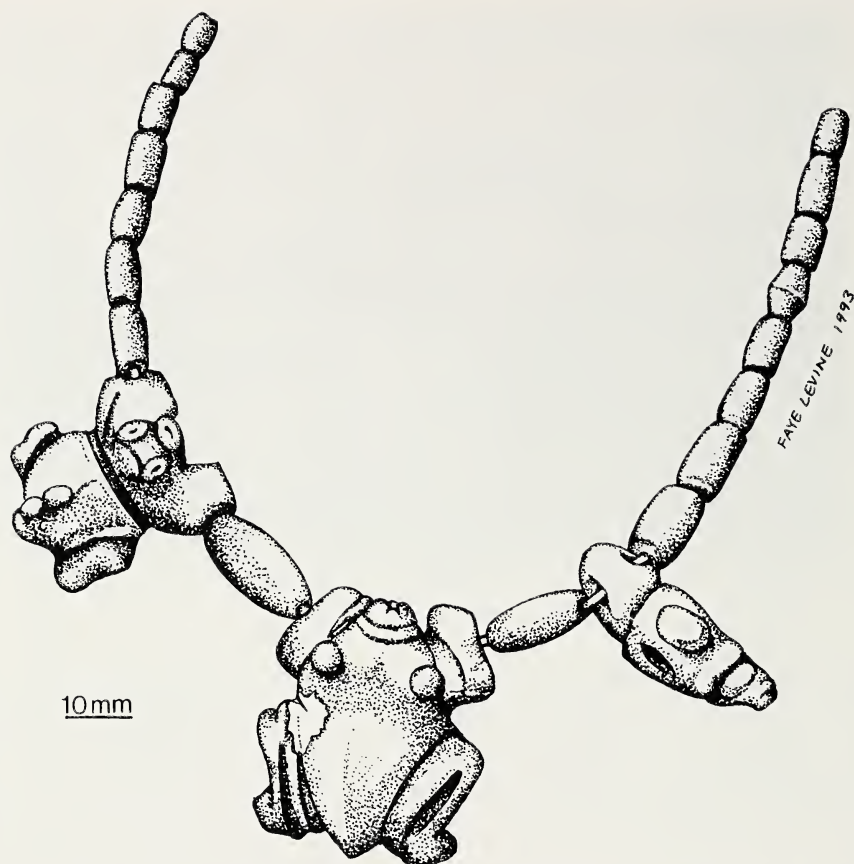


Fig. 4.—A prehistoric necklace from Guadeloupe displaying both beads and pendants (adapted from Durand and Petitjean Roget, 1991:plate II).

DESCRIPTIVE ANALYSIS

For the purposes of this study, a coding scheme of 17 variables was devised, not all of which pertained to every artifact category. In fact, “material” was the only variable that could be coded for all artifacts.

Rocks and minerals comprising the beads and pendants were first discussed by Harrington (1924), who concentrated on the “semi-precious stones,” and subsequently by Ball (1941), in a survey of gem and ornamental stone mining in the New World. Harrington’s material attributions (Table 3) appear to have been based on his own knowledge and judgment rather than mineralogical or gemological tests. Judging by his virtually identical materials list, Ball (1941:17 and table 1) apparently relied on Harrington’s identifications. The MAI catalog cards for the Howes collection list a greater variety of materials (Table 3).

Neither catalog numbers nor artifact illustrations are provided by Harrington and Ball; therefore, it is not possible to assign their attributions to specific artifacts. Our overall material categories are similar to theirs, but we were unable to verify examples of two of their identifications: lapis lazuli and cannel coal. In this paper,

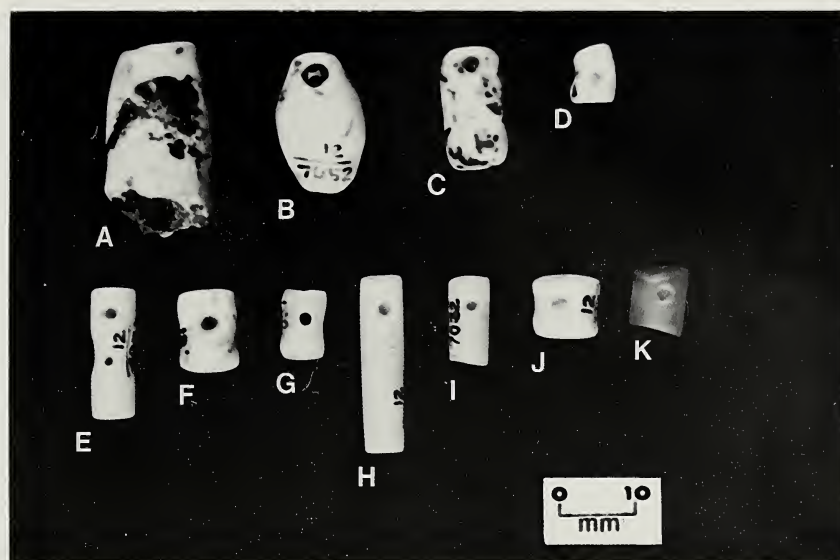


Fig. 5.—The 11 double-perforated objects having longitudinal and transverse perforations. A, 12/7035(001); B, 12/7052(001); C, 12/7033(001); D, 12/7120(078); E, 12/7031(003); F, 12/7031(002); G, 12/7031(001); H, 12/7032(002); I, 12/7032(001); J, 12/7030(001); K, 12/7028(001). A–D are diorite (material 25); E–J are unidentified (material 22), possibly quartzite; K is unidentified (material 16).

our material attributions accompany the MAI catalog numbers (e.g., 12/7011) in the captions of artifact photographs.

Table 4 presents a frequencies analysis for 29 categories of lithic materials. Five materials (Table 5) tested and identified by the GIA Gem Trade Laboratory include carnelian, amethyst, turquoise, nephrite jade, and quartzite (Gemological Institute of America, 1985). Our use of specific names reflects *reasonable confidence* in identification. Less secure attributions are qualified as *probable* or *possible*; unidentified materials are described.

In order to present a more consolidated table, the “certainty levels” were collapsed, combining the “reasonably confident” and “probable” attributions under their appropriate material labels, and combining “possible” and “unidentified” as simply “unidentified.” Results are presented in Table 6.

Raw Materials

The simplest category of objects, raw materials, represents the “first stage” of the manufacturing process. These specimens are unformed pieces of materials showing no clear evidence of shaping (Fig. 7). A breakdown of these objects by material is presented in Table 7, which shows that 90% of the specimens are carnelian.

Bead Blanks

Bead blanks are objects whose shape and geometry resemble those of beads, but which have no perforations or unfinished perforations (Fig. 7). The materials represented by these 72 objects are grouped in Table 8. It should be noted that



Fig. 6.—Materials represented by bead blanks. A, carnelian (material 1; 12/7011), the most common; B, unidentified (material 31; 12/7041), possibly feldspar; C, diorite (material 25; 12/7042); D, quartz (material 55; 12/7051).

Table 3.—Previous material attributions of the Howes collection beads and pendants.

Material attribution	Harrington (1924)	Ball (1941)	MAI catalog cards ^a
Carnelian	x	x	x 12/7011
Amethyst	x	x	x 12/7016
Chalcedony	x	x	x 12/7040
Quartz (rock) crystal	x	x	x 12/7050
Turquoise	x	x	x 12/7026
Cannel coal	x	x	x 12/7063
Lapis lazuli	x	x	
Nephrite	x	x	
Jade	x		x 12/7073
Jadeite		x	
Agate	x		
Serpentine			x 12/7023
Feldspar			x 12/7029
Altered granitic rock			x 12/7033
Quartz			x 12/7039
Petrified wood			x 12/7062
Chalcedony/calcite/gypsum			x 12/7051
Marble			x 12/7060
Soap stone			x 12/7069
Green (amazon) stone			x 12/7064
White stone			x 12/7030
Brown stone ^b			x 12/7045
Gray stone			x 12/7083

^a In some instances, only one of several catalog card numbers is used to exemplify the material attribution.

^b This brown stone bead actually is a ceramic bead.

69.4% of bead blanks are carnelian. The relatively high proportion of broken to unbroken bead blanks (24/48) could be interpreted as breakage sustained during the manufacturing process.

Beads

Most specimens in the MAI collections are completed beads. Following Beck (1981), they were divided into regular rounded and regular faceted subtypes.

Regular Rounded Beads.—Regular rounded beads comprise 360 of the 503 specimens or 71.6% of the total objects. At least six materials are represented among the 354 lithic regular rounded beads (Table 9), but the vast majority of these are diorite (71.2%). Only 1.1% of the finished regular rounded beads are carnelian. Since 90.0% of raw materials and 69.4% of bead blanks are carnelian, a much greater proportion of carnelian in the finished objects might have been expected.

The lengths of the beads are highly variable (Fig. 8, 9, 10). Interestingly, the lengths of the blanks ($n = 50$; mean = 23.84; SD = 8.20; coefficient of variation = 0.34) are more homogeneous than the lengths of the finished beads ($n = 320$; mean = 13.25; SD = 6.99; coefficient of variation = 0.53). This homogeneity of bead blanks is suggestive of a specialized local manufacturing industry. Regular rounded beads should ideally be symmetrical; thus, end diameters should be virtually identical on individual beads. The fact that the mean end diameters in this sample do not differ significantly ($t = -0.317$, $P > 0.37$) suggests relative precision in the manufacture of these particular objects.

Table 4.—*Lithic materials: frequencies.*

Material category no.	Description or identification	Frequency	Percentage
25	diorite	260	53.1
1	carnelian	76	15.5
64	translucent, high gloss; probably rock crystal or glass	38	7.8
4	amethyst	22	4.5
10	green and blue-green with reflective flecks; probably aventurine	13	2.7
89	whitish gray (some banded), opaque, some luster	12	2.4
13	turquoise	11	2.2
31	white, opaque, no luster; possibly feldspar	10	2.0
28	white, little luster, no apparent black; probably diorite	8	1.6
55	rock crystal (translucent, medium gloss)	7	1.4
22	white, opaque, no luster; possibly quartzite	6	1.2
46	white, opaque, no luster; possibly limestone	5	1.0
49	light green, low gloss	3	0.6
70	greenish gray, medium gloss; probably nephrite or jadeite	3	0.6
73	white, opaque, no luster	2	0.4
16	light green, translucent	1	0.2
19	green, brown patina, no luster; possibly turquoise	1	0.2
34	black and white with red inclusions; probably diorite	1	0.2
37	pink, dark inclusions, high gloss	1	0.2
43	black, fine grain, medium luster	1	0.2
52	rock crystal (translucent, high gloss)	1	0.2
61	rock crystal (transparent, high gloss)	1	0.2
67	dark green, striated; probably serpentine	1	0.2
76	green, medium luster; probably nephrite or jadeite	1	0.2
79	nephrite	1	0.2
82	dark gray, slight luster; probably serpentine	1	0.2
85	light pink, opaque	1	0.2
95	red, opaque; possibly carnelian	1	0.2
98	greenish blue with brown inclusions, opaque, no luster	1	0.2
Totals		490	100.0

The general shape categories established by Beck (1981:5–6, plate 1) were used to describe the transverse sections of beads (Fig. 11). Regular rounded beads and bead blanks are of only two basic types, circular and elliptical, with the overwhelming majority (97.1% of bead blanks and 99.7% of finished beads) being circular. The infrequency of the elliptical shapes in both beads and blanks suggests that the few specimens merely represent errors in manufacture. The profiles or

Table 5.—*Gemologically verified materials in the Howes collection.*

Material identification ^a	Specimen number ^b	Remarks ^c
Carnelian	12/7012(005) ^d	material 1
Amethyst	12/7017(001)	material 4
Turquoise	12/7026(004)	material 13
Turquoise	12/7065(001)	material 13
Nephrite jade	12/7084(001)	material 79
Quartzite	12/7031(001)	material 22

^a GIA Gem Trade Laboratory, Gem Identification Report #1926912, 19 April 1985.

^b MAI catalog number followed by the piece number (in parentheses) assigned by Watters.

^c Material numbers assigned by Watters (see Table 4).

^d The GIA report erroneously lists this as 12/7022.

Table 6.—*Lithic materials: collapsed frequencies.*

Material category nos.	Probable material	Frequency	Percentage
25, 28, 34	diorite	269	54.9
1	carnelian	76	15.5
64, 55, 52, 61	rock crystal	47	9.6
4	amethyst	22	4.5
10	adventurine	13	2.7
13	turquoise	11	2.2
70, 76, 79	jade group	5	1.0
67, 82	serpentine	2	0.4
89, 31, 22, 46, 49, 73, 16, 19, 37, 43, 85, 95, 98	unidentified	45	9.2
Totals		490	100.0

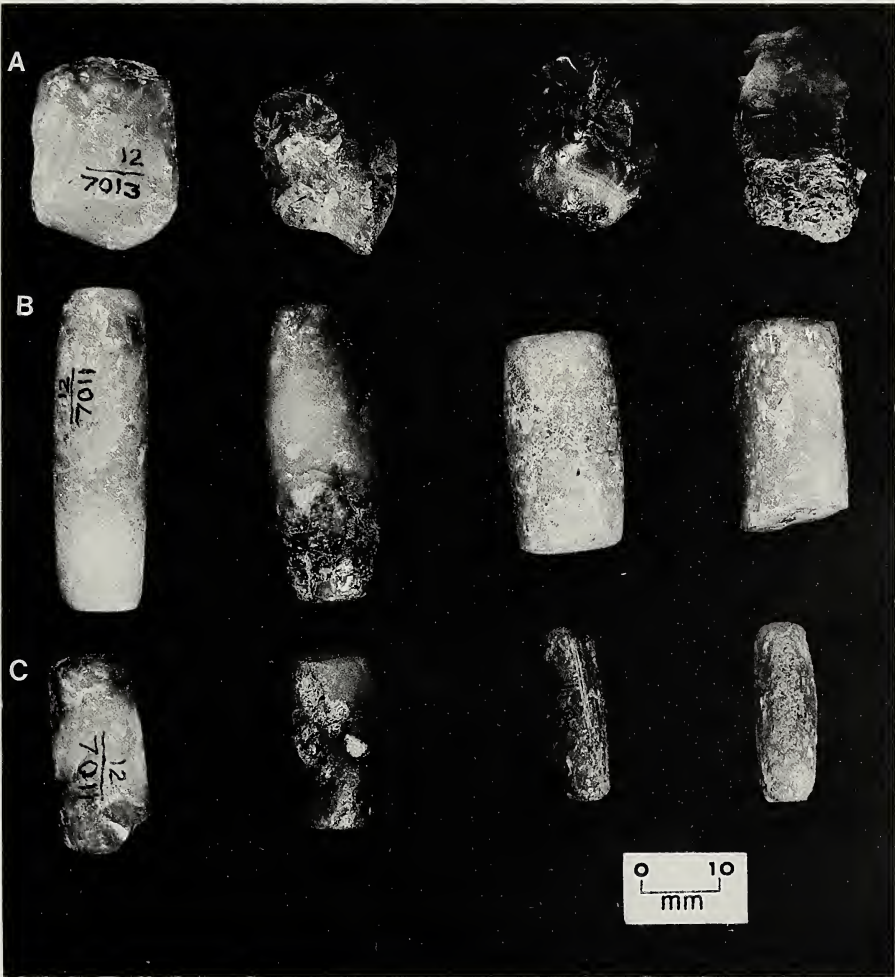


Fig. 7.—Carnelian (material 1) objects. A, four raw material specimens (12/7013); B–C, eight bead blanks in various stages of the manufacturing process (12/7011).

Table 7.—*Raw materials: frequencies.*

Material category nos.	Probable material	Frequency	Percentage
1	carnelian	18	90.0
55, 61	rock crystal	2	10.0
Totals		20	100.0

“side views” of beads were also based on Beck (1981:7–9, plates II and III). Convex (barrel) and straight (cylinder) profiles constitute the overwhelming majority (97.7%) of regular rounded beads (Table 10, Fig. 12) and constitute exclusively the bead blanks.

Regular Faceted Beads.—Whereas the perimeter of the transverse section of a regular rounded bead is curvilinear, the perimeter of a regular faceted bead is a polygon. Most transverse sections of regular faceted beads are hexagonal (Fig. 11, Table 11). The two regular faceted bead blanks are pentagonal and “polygonal,” the latter a category used by Beck (1981:6). It is possible that faceted beads (particularly those whose transverse sections are multisided polygons) are not really a “type” of bead, but rather a “stage” in the manufacturing process and/or are poorly-made regular rounded beads. Data on the longitudinal sections or “side view profiles” of regular faceted beads are compiled in Table 12, and the material frequencies analysis is presented in Table 13. Two blanks, both broken, are rock crystal and an unidentified material, although the most common material for both regular faceted and regular rounded beads is diorite. However, faceted beads made of carnelian are proportionally more common.

Pendants

Pendants typically have distinctive forms, very often being zoomorphic representations (Fig. 13). A materials breakdown shows that the “jade group” (jadeite, nephrite) constitutes some 41.6% of the sample (Table 14). Pendants are the only category of artifacts manufactured from jade group materials. (Pendants on display at the MAI Manhattan facility, although not part of this study, also had a high proportion of green-colored stones possibly belonging to the jade group.) Turquoise is also heavily represented in studied pendants (25%) as compared with, for example, regular rounded beads (2%). Clearly, there is a high proportion of “exotic” materials represented in pendants. The only pendant blank with a material attribution is serpentine. It and a finished pendant are the only representatives of serpentine among all the lithic objects.

Table 8.—*Bead blanks: frequencies.*

Material category nos.	Probable material	Frequency	Percentage
1	carnelian	50	69.4
25	diorite	7	9.7
31	unidentified	7	9.7
64, 55	rock crystal	7	9.7
95	unidentified	1	1.4
Totals		72	100.0

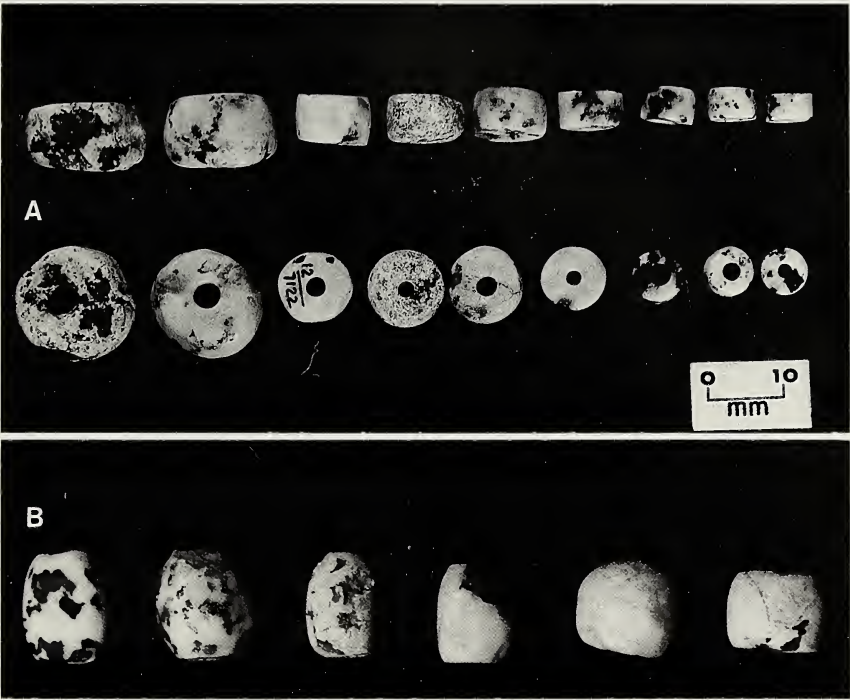


Fig. 8.—Diorite (material 25) beads, the most common material for regular rounded beads. A, longitudinal and transverse views of the same short to disc beads (12/7122); B, longitudinal view of standard to short beads (12/7121) (see Fig. 11).



Fig. 9.—Size range in regular rounded quartz (rock crystal) beads (material 64; 12/7056 and 12/7057). The large specimen (material 52; 12/7049) in the lower right is a truncated bicone.



Fig. 10.—Regular rounded beads provisionally attributed to aventurin (material 10; 12/7023 and 12/7024).

DISCUSSION

The only locational information on the MAI catalog cards for the S. W. Howes collection is "Montserrat, British West Indies." However, Mrs. van der Veer and Bruce Howes are confident that their father collected artifacts only on the Trants Estate. In the tilled fields, S. W. Howes also found historic beads (some of which are still in Mrs. van der Veer's possession) but these were of no interest to the MAI. Nevertheless, seven historic beads (Table 2), all made of glass, were included in the materials sent to the MAI because superficially they resembled certain prehistoric lithic beads collected by Howes. It is also possible that a few of the lithic beads, all of which are assumed to be prehistoric in origin, may date to the historic period of use of the Trants Estate.

Because the artifacts were surface collected, they lack contextual, stratigraphic, or other provenience data. Fortunately, beads and related lithics were found in undisturbed prehistoric contexts during excavations in 1979 and 1990. Materials represented in the excavated objects include carnelian, diorite, amethyst, quartz, feldspar, and jadeite or nephrite, as well as several unidentified materials (Bartone and Crock, 1991).

Comparatively high frequencies of exotic (nonlocal) lithic artifacts have been

Table 9.—*Regular rounded beads: frequencies.*

Material category nos.	Probable material	Frequency	Percentage
25, 28, 34	diorite	252	71.2
64, 52	rock crystal	37	10.5
4	amethyst	20	5.6
10	adventurin	11	3.1
89	unidentified	10	2.8
13	turquoise	7	2.0
46	unidentified	5	1.4
1	carnelian	4	1.1
31	unidentified	3	0.8
49	unidentified	3	0.8
19	unidentified	1	0.3
43	unidentified	1	0.3
Totals		354	100.0

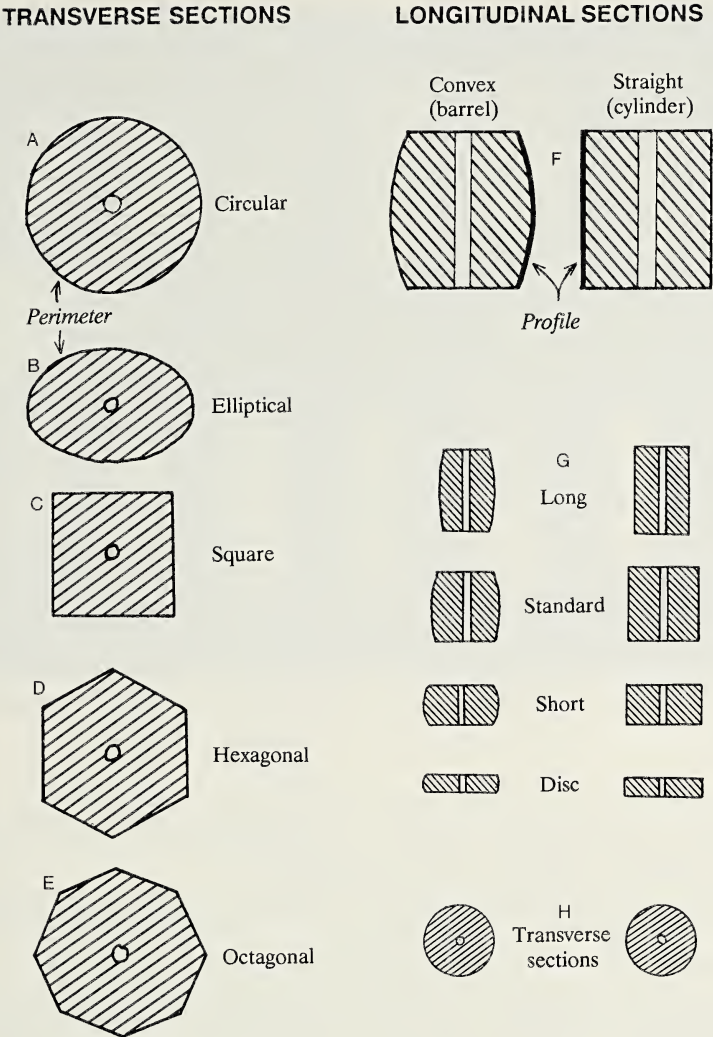


Fig. 11.—Drawings illustrating some of the classifications and terms used in this paper (adapted from Beck, 1981:plates I, II, and III, and fig. 2, 3). A–B, transverse sections of regular rounded beads; C–E, transverse sections of regular faceted beads; F, longitudinal sections of regular rounded beads; G, Beck’s terms for classifying regular rounded beads by length; H, all eight beads illustrated in G have circular transverse sections.

reported on at least four islands in the region—Vieques Island, near Puerto Rico (Chanlatte Baik and Narganes Storde, 1983; Chanlatte Baik, 1984), St. Croix, U.S. Virgin Islands (Vescelius and Robinson, 1979; Faber Morse, 1989:fig. 4e–f), Montserrat (Harrington, 1924), and Grenada (Cody, 1990, 1991a, 1991b). There are reports of exotic lithics on other islands, among them St. Vincent (Bullen and Bullen, 1972:plate XIXf), Barbados (Drewett, 1991:132), Martinique (Mattioni, 1979:49), Guadeloupe (Clerc, 1970:fig. 27; Durand and Petitjean Roget, 1991), Nevis (Wilson, 1989:436), St. Kitts (Fewkes, 1922:165, plate 85f), St. Martin (Haviser, 1993), St. Eustatius (Versteeg and Schinkel, 1992:fig 160), and

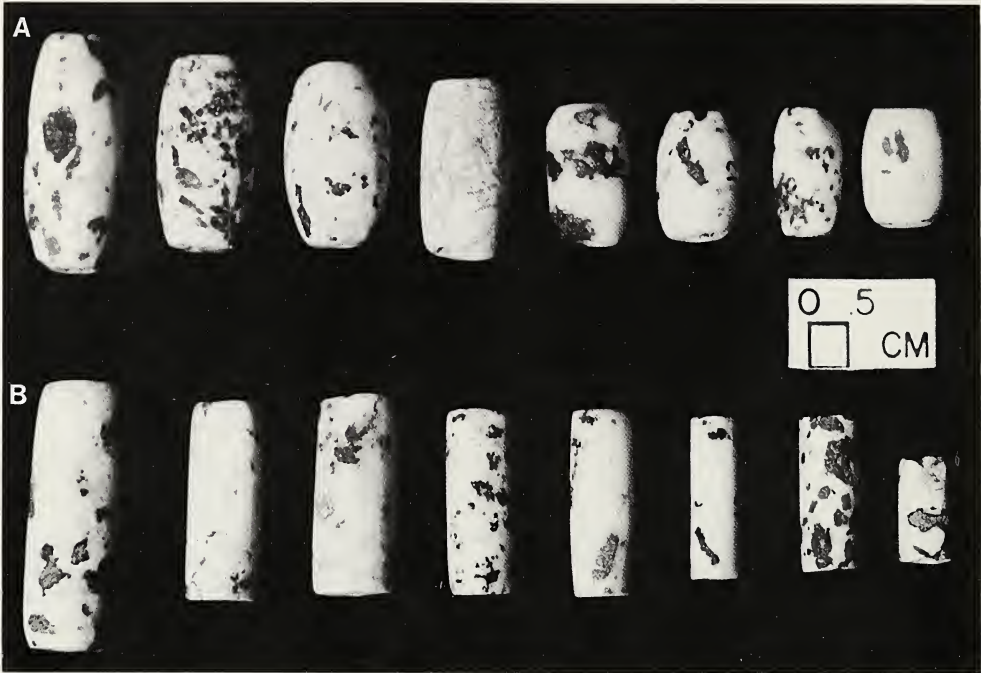


Fig. 12.—Diorite (material 25) beads (12/7119). A, convex or “barrel” beads; B, straight or “cylinder” beads.

Puerto Rico (Rouse and Alegría, 1990:50, fig. 12, plate 11; Rodríguez, 1991:610–612; Rodríguez and Rivera, 1991:fig. 6, 7). Sued Badillo (1978) discusses the prehistoric lapidary industry in the Caribbean.

Many of the lithic materials in the S. W. Howes collection from Montserrat are duplicated in the collections from Vieques, St. Croix, and Grenada, but there are some intriguing differences. Although there is no known source for carnelian on Montserrat, it is represented in all stages of manufacture in the Howes collection, and is also disproportionately represented in the excavated artifacts from Trants, where it comprises 65% of bead debitage and 88% of the blanks (Bartone and Crock, 1991). Furthermore, two of the three Howes collection bead blanks ex-

Table 10.—*Regular rounded beads: frequencies.*

Longitudinal section category nos.	Shape	Frequency	Percentage
12	convex (barrel)	188	53.1
21	straight (cylinder)	158	44.6
25	straight (truncated bicone)	4	1.1
11	convex (oblate, circular, ellipsoid)	1	0.3
15	convex (bicone)	1	0.3
19	convex (wedge) ^a	1	0.3
23	straight (truncated cone)	1	0.3
Totals		354	100.0

^a The convex (wedge) category was added by the authors; it is not used by Beck (1981).

Table 11.—*Regular faceted beads: frequencies.*

Transverse section category nos.	Shape	Frequency	Percentage
13	hexagonal	13	76.5
14	octagonal	2	11.8
9	square	2	11.8
Totals		17	100.0

Table 12.—*Regular faceted beads: frequencies.*

Longitudinal section category nos.	Shape	Frequency	Percentage
21	straight (cylinder)	10	55.6
23	straight (truncated cone)	2	11.1
12	convex (barrel)	2	11.1
16	convex (truncated bicone)	1	5.6
24	straight (bicone)	1	5.6
25	straight (truncated bicone)	1	5.6
26	straight (chamfered cylinder)	1	5.6
Totals		18	100.0

Table 13.—*Regular faceted beads: frequencies.*

Material category nos.	Probable material	Frequency	Percentage
25	diorite	6	33.3
1	carnelian	4	22.2
4	amethyst	2	11.1
10	adventurine	1	5.6
13	turquoise	1	5.6
64	rock crystal	1	5.6
89, 37	unidentified	3	16.7
Totals		18	100.0

Table 14.—*Pendants: frequencies.*

Material category nos.	Probable material	Frequency	Percentage
70, 76	jade group	4	33.3
13	turquoise	3	25.0
73	unidentified	2	16.7
10	adventurine	1	8.3
79	nephrite	1	8.3
82	serpentine	1	8.3
Totals		12	100.0

changed with the University Museum (Table 1) are carnelian. At Trants, carnelian is found in all stages of lithic reduction, whereas amethyst occurs only as finished beads (Fig. 14). Cody (1991a) documents just the opposite on Grenada, where amethyst beads are found in all stages of manufacture, but carnelian occurs only as finished beads.

There very likely are geological sources within the West Indies for some of the materials, such as serpentine and diorite, recognized both in the Howes collection



Fig. 13.—Pendants in the S. W. Howes collection. Front and back views: A, 12/7084(001), material 79, nephrite (verified gemologically); B, 12/7083(001), material 76, “jade group”; C, 12/7088(001), material 82, probably serpentine; D, 12/7069(001), material 70, “jade group”; E, 12/7074(001), material 70, “jade group”; F, 12/7075(001), material 73, unidentified. Single views: G, 12/7078(001), material 13, turquoise; H, 12/7066(001), material 70, “jade group”; I, 12/7067(001), material 10, probably aventurin; J, 12/7064(001), material 13, turquoise; K, pendant blank, 12/7068(001), material 98, unidentified. The best quality pendants, being on exhibit, were not available for study.

and in collections from other sites in the region. However, there are no known West Indian sources for turquoise (Fig. 15) and the “jade group.” Cody (1990, 1991b) reports only two sources of turquoise in South America: northern Chile and eastern Brazil. South American sources for the “jade group” (more generally termed “greenstone”) have been investigated in considerable detail because of the importance of greenstone pendants among surviving indigenous groups (Boomert, 1987). Greenstone artifacts in the Lesser Antilles are most commonly associated with the Saladoid ceramic series, which is generally interpreted as the earliest of the Ceramic Age population movements into the region.

The S. W. Howes collection thus contains an unusually rich assemblage of prehistoric beads and pendants of diverse types manufactured from a wide range of materials (Fig. 16) that adds to existing knowledge of the prehistoric lapidary industry in the Lesser Antilles.

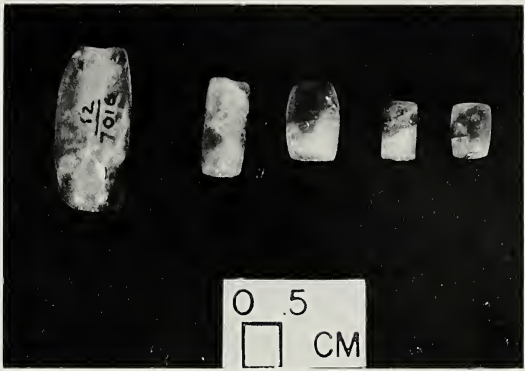


Fig. 14.—Only finished amethyst beads (material 4; 12/7016) were recovered at Trants.

CONCLUSIONS

The evidence provided by the beads in the Howes collection, coupled with information regarding excavated beads, strongly suggests that Trants was a pre-historic lithic bead manufacturing site specializing in carnelian beads. The relatively high proportion of broken blanks is compatible with this interpretation, and the homogeneous nature of bead blanks provides additional evidence of a specialized manufacturing industry.

Carnelian seems to have been the most common material used for the local manufacture of lithic beads, despite an absence of known local sources. Diorite and rock crystal are also represented in early manufacturing stages. Whereas 90.0% of raw materials and 69.4% of bead blanks are carnelian, only 1.1% of finished beads were of this material, suggesting probable import of raw materials and off-island trade of the finished products. It may be that certain islands in the Lesser Antilles, such as Montserrat (carnelian) and Grenada (amethyst) were specializing in the production of lithic beads primarily for off-island trade. If so, the identification of other island manufacturing sites would provide important clues for understanding interisland interaction in Caribbean prehistory.

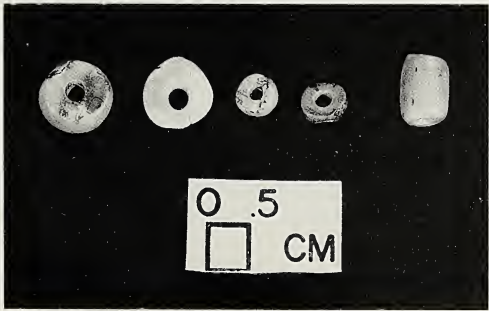


Fig. 15.—Five turquoise beads (material 13; 12/7026 and 12/7027). The disc head on the left, 12/7026(004), was the specimen tested and identified as turquoise by the GIA Gem Trade Laboratory.

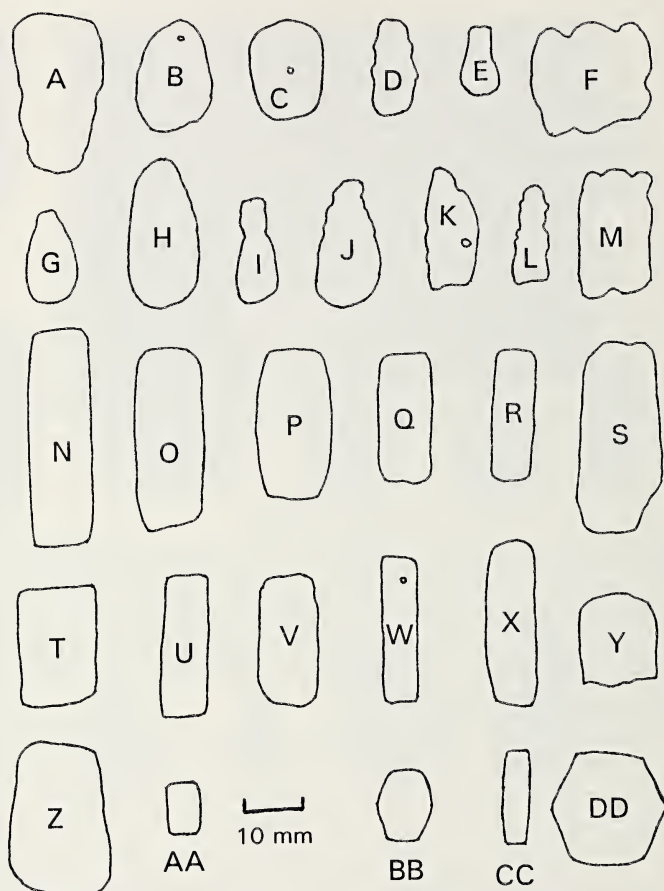
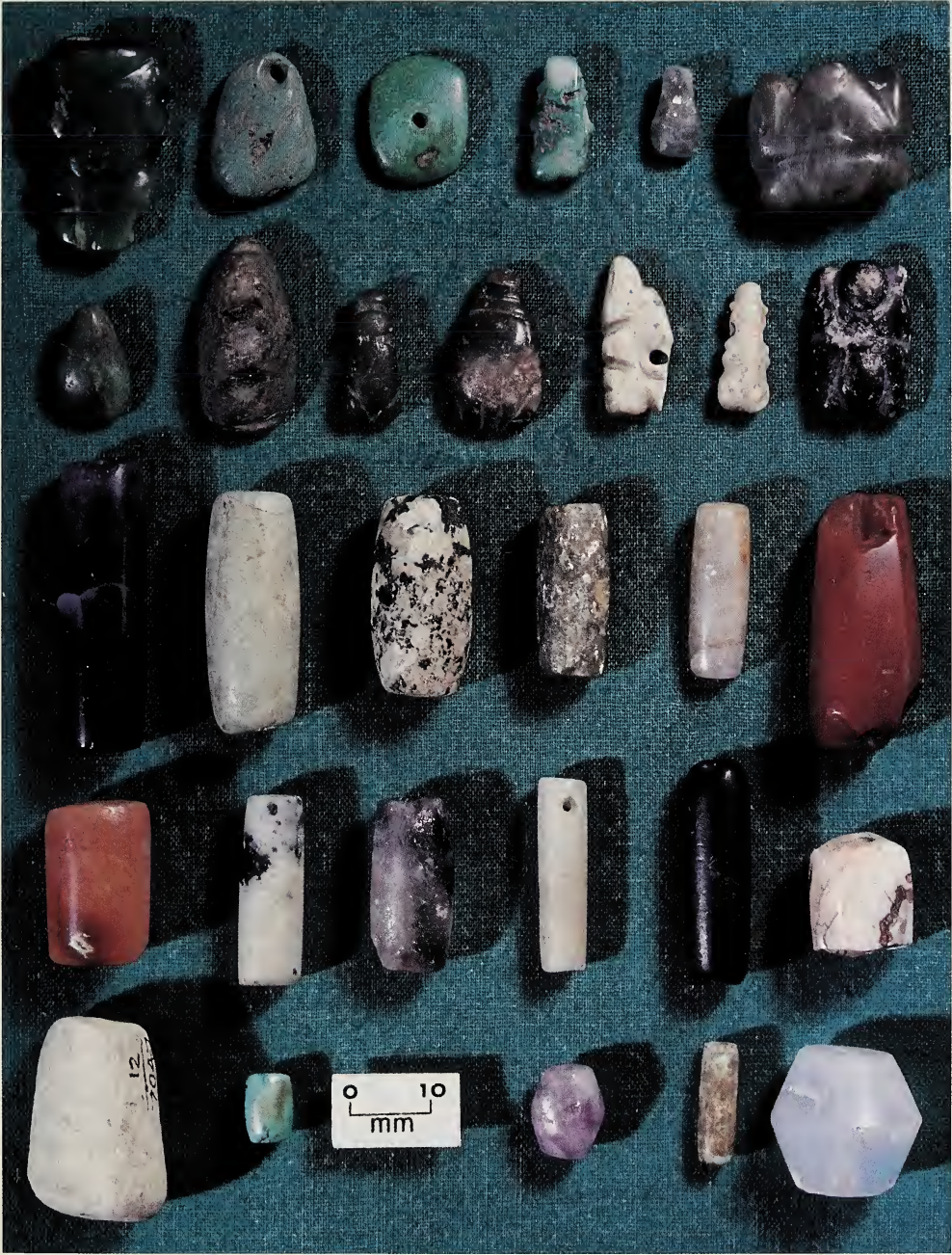


Fig. 16.—Pendants and beads in the S. W. Howes collection. A, 12/7084(001), material 79 (nephrite; specimen verified gemologically); B, 12/7064(001), material 13 (turquoise); C, 12/7065(001), material 13 (turquoise; verified gemologically); D, 12/7078(001), material 13 (turquoise); E, 12/7067(001), material 10 (probably adventurine); F, 12/7083(001), material 79 ("jade group"); G, 12/7066(001), material 70 ("jade group"); H, 12/7068(001), material 98 (unidentified); I, 12/7074(001), material 70 ("jade group"); J, 12/7069(001), material 70 ("jade group"); K, 12/7076(001), material 73 (unidentified); L, 12/7075(001), material 73 (unidentified); M, 12/7088(001), material 82 (probably serpentine); N, 12/7017(001), material 4 (amethyst quartz; verified gemologically); O, 12/7048(004), material 49 (unidentified); P, 12/7119, material 25 (diorite); Q, 12/7023(003), material 10 (probably adventurine); R, 12/7056, material 64 (probably rock crystal quartz); S, 12/7012(006), material 1 (carnelian; possibly a historic bead); T, 12/7012(002), material 1 (carnelian); U, 12/7119, material 25 (diorite); V, 12/7016(012), material 4 (amethyst quartz); W, 12/7032(002), material 22 (unidentified, possibly quartzite; double-perforated object); X, 12/7046(001), material 43 (unidentified); Y, 12/7044(001), material 37 (unidentified); Z, 12/7047(002), material 46 (possibly limestone); AA, 12/7027(001), material 13 (turquoise); BB, 12/7021(001), material 4 (amethyst quartz); CC, 12/7029(001), material 19 (possibly turquoise); DD, 12/7049(001), material 52 (rock crystal quartz). Three beads (P, R, U), all of which are associated with MAI catalog numbers containing numerous specimens, lack recorded piece numbers (in parentheses).



ACKNOWLEDGMENTS

Watters' research at the Museum of the American Indian (MAI), Heye Foundation, in New York was supported by the Netting Research Fund of Carnegie Museum of Natural History (CMNH). The authors acknowledge the assistance of James B. Petersen, who studied the Howes collection ceramics; Stanley W. Lantz for his extensive photographic documentation of the collection; Carrie Pantier for darkroom assistance; staff members Anna C. Roosevelt, Mary Jane Lenz, Eulie Wierdsma, and Nancy Rosoff of the Museum of the American Indian for help accessing the collection; Queenie Howes van der Veer and Bruce Howes for discussing their childhood recollections of Trants Estate and for permission to reproduce personal photographs of S. W. Howes and his home; Marc L. Wilson, Collections Manager of the CMNH Section of Minerals, for discussing mineral nomenclature and classification; Sylvia Keller and Colleen Mylan for assisting with manuscript preparation; and the three anonymous reviewers for their careful reading and insightful comments. Research in 1985 took place at the Research Branch in the Bronx when it was a facility of the Museum of the American Indian, Heye Foundation, and in 1991 when it was part of the National Museum of the American Indian, Smithsonian Institution. We have opted to use the MAI catalog numbers in this report since that organization originally acquired and cataloged the S. W. Howes collection.

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A PRIMITIVE CRICETID (MAMMALIA: RODENTIA) FROM THE MIDDLE EOCENE OF JIANGSU PROVINCE, CHINA

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ABSTRACT

A new species of the cricetid rodent *Pappocricetodon*, *P. antiquus*, from Middle Eocene fissure deposits in southeastern China combines such derived features as uniserial incisor enamel and a hystricomorphous zygomatic structure with primitive characters including retention of P⁴ and less expansion of the anterocone/id of M¹/M₁ than in other species of the genus. This addition to the Eocene record of myomorph rodents lends support to the hypothesis that the most likely sister group of the Myomorpha is the family Sciuravidae.

INTRODUCTION

The Cricetidae, one of the most flourishing families of living rodents in the world, are known to have diversified and dispersed in the Holarctic since latest Eocene times. Due to their abundance in the fossil record, cricetids have been used in the subdivision and correlation of Cenozoic Holarctic continental deposits (Fahlbusch, 1964; Mein, 1975; Engesser, 1985). This abundance has also led to numerous investigations of evolution within the family (Mein and Freudenthal, 1971a; Lindsay, 1968, 1977; Martin, 1980). Although the origin and interrelationships of the cricetids have been discussed frequently, the source of the family has been unclear. Suggested relationships have been with the Sciuravidae (Schaub, 1925; Wilson, 1949b; Wood, 1959; Martin, 1980; Walton, 1993) or with the ctenodactylids (Lindsay, 1977; Flynn et al., 1985; Vianey-Liaud, 1985; Wang and Meng, 1986).

Part of the difficulty of studying the origin of the family has been the lack of good middle and early late Eocene records for the family. For many years this record consisted of two lower molars referred to *Cricetodon schaubi* from the Late Eocene River Section of Shanxi Province, China (Zdansky, 1930). Recently, the new genus *Pappocricetodon* was described from China, with two species: *P. rencunensis* from the late middle Eocene (Rencun Member, Hedi Formation) of Henan; and *P. schaubi*, for Zdansky's species, from the late Eocene (Zhaili Member, Hedi Formation) of Shanxi (Tong, 1992).

From 1987 to 1992 a field party from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Academia Sinica (Qi et al., 1991), and, from 1993, a cooperative field team from the IVPP and the Carnegie Museum of Natural History (CM) collected a variety of fossil mammals from fissure fillings in the Triassic Shangqinglong Limestone in the Shanghuang Quarry of Liyang County, Jiangsu Province, China (Fig. 1). To date five fissures (IVPP Locs. 93006.A-E)

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Submitted 18 February 1994.

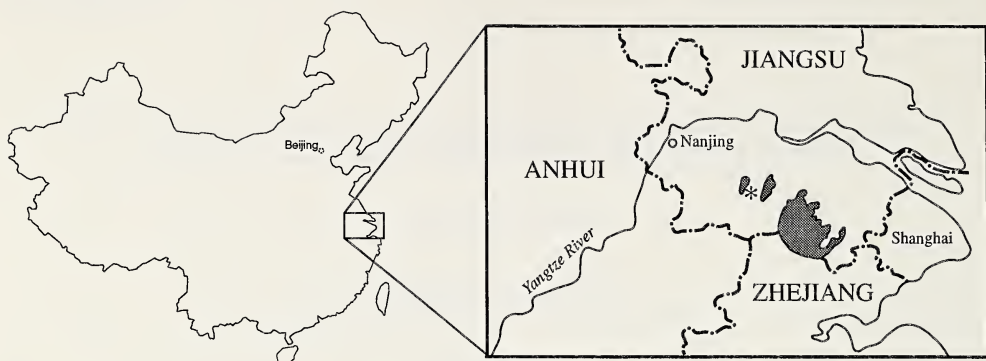


Fig. 1.—Map of China with enlargement showing parts of Jiangsu and adjoining provinces and location (*) of Shanghuang Quarry, Liyang County.

have been found to contain Paleogene deposits. In Fissure D (IVPP Loc. 93006.D) the deposits, composed mostly of red clay with lesser amounts of yellow clay, are rich in fossil mammals. Cricetid fossils dominate in Fissure D. In addition to the cricetids, the fossil mammals include varied insectivores, omomyids, leporids, *Yuomys* sp., ctenodactyloids, creodonts, *Archaeomeryx* sp., Anthracotheriidae, Homacodontidae, *Eoentelodon*, cf. *Helohyus*, brontotheres, palaeotheres, and tapiroids. All the specimens were collected by quarrying followed by screen washing. The total mammal fauna from Fissure D suggests a middle Eocene age. The Cricetidae is represented by the most primitive known and probably oldest member of the family, described here as a new species of *Pappocricetodon*.

The discovery of this primitive cricetid from the middle Eocene both reveals some primitive features and provides some suggestions on the origin of the Cricetidae and on evolutionary trends within the family.

METHODS

Figure 2 illustrates basic terminology used here for cricetid molars, combining conventional rodent dental terminology (e.g., Wood and Wilson, 1936; Mein and Freudenthal, 1971*b*) with nomenclature necessitated by the primitive features of these rodents and the opportunity to employ terms suggesting dental homology. For example, on M^1 the crest that extends anterobuccally from the protocone is termed protoloph, instead of "anterior arm of protocone" (Fahlbusch, 1964; Vianey-Liaud, 1979) because it appears homologous to the protoloph of more primitive rodents such as sciuravids. The cusp on the lingual part of the anterior cingulum, the anterocone of Lillegraven and Wilson (1975), is named the anterostyle, and their parastyle is named the anterocone. "Mure" is used for the anterior arm of the hypocone whether or not it joins the protocone. The "sinus" of the upper molar (Mein and Freudenthal, 1971*b*; Vianey-Liaud, 1979) is called "lingual valley." On the lower molars the anterior arm of the protoconid is termed the protolophid and the buccal crest of the metaconid, the metalophid.

Biostratigraphic terminology for Oligocene localities follows Wang (1992) as the most recent treatment of this interval in Asia.

Measurements were all taken by Wang using a micrometer in a Wild binocular microscope. For consistency only the left side was measured for well-represented teeth; the scarcer $M3/3$ were all measured.

In the tooth descriptions, frequency of a character variant is expressed as a ratio, with the upper number indicating presence of the variant and the lower number, total number of specimens showing the character. Thus, 101/143 indicates that out of 143 specimens, 101 have the variant described.

Abbreviations for repositories are: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology. Tables of measurements (in millimeters, mm) of the dentition utilize the positional abbreviations: L, length;

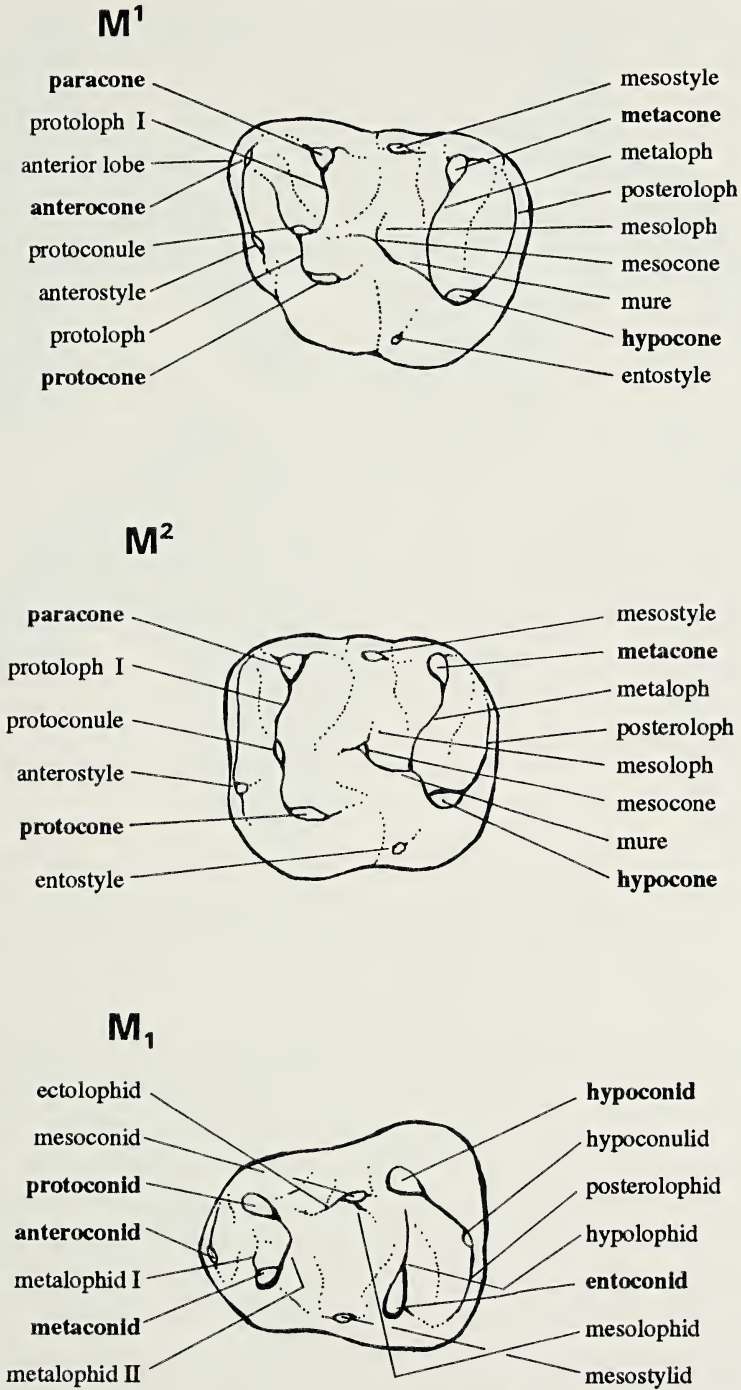


Fig. 2.—Terminology used for cricetid molars, showing simplified left M¹ and M², and right M₁.

W, width; b, buccal; l, lingual. For statistical treatment, abbreviations used are: *n*, number of specimens; O.R., observed range; \bar{x} , mean; *s*, standard deviation; C.V., coefficient of variation.

SYSTEMATICS

Order Rodentia Bowdich, 1821

Superfamily Muroidea Miller and Gidley, 1918

Family Cricetidae Rochebrune, 1883

Pappocricetodon Tong, 1992

Pappocricetodon antiquus, new species

(Table 1)

Holotype.—LM¹ (IVPP V 11018.1).

Referred Specimens.—142 M¹ (IVPP V 11018.2–V 11018.143), 144 M² (IVPP V 11018.144–V 11018.287), 21 M³ (IVPP V 11018.288–V 11018.308), one left lower jaw with I₁ and M₁ (IVPP V 11018.309), one left lower jaw with M₁ (IVPP V 11018.310), one right lower jaw with M₁₋₂ (IVPP V 11018.311), 111 M₁ (IVPP V 11018.312–V 11018.422), 151 M₂ (IVPP V 11018.423–V 11018.573), 30 M₃ (IVPP V 11018.574–V 11018.603), 4 maxillae (IVPP V 11018.604–V 11018.607), 3 lower jaws (IVPP V 11018.608–V 11018.610) and 2 I₁ (IVPP V 11018.611–V 11018.612).

Diagnosis.—Cricetid smaller than *P. rencunensis*, with hystricomorphous skull and sciurognathous lower jaw; dental formula: 1/1, 0/0, 1/0, 3/3; cheek teeth brachydont; upper molars have protocone bulbous and mesoloph short; M¹ less enlarged, having anterior lobe weak and anterocone small, protoloph I weak and usually connecting to protoloph, protoloph II absent; on M¹⁻² mure usually long, lingual valley long and oblique; M³ less reduced than in other species of genus, with distinct metacone and somewhat reduced but less buccad hypocone; lower molars usually lacking ectomesolophid; M₁ less enlarged with anteroconid small and usually isolated; on M₁₋₂ hypolophid transverse, connecting to hypoconid or its posterior arm; lower incisor with uniserial enamel.

Etymology.—From Latin, *antiquus*, ancient, old.

Description.—Four edentulous maxillae of *Pappocricetodon antiquus* show that the infraorbital foramen is relatively large and rounded with no ventral constriction. This is the hystricomorphous condition. There is no bony septum isolating a neurovascular canal such as occurs in dipodoids. The ventral root of the zygomatic process extends laterally well anterior to P⁴ and is compressed dorso-ventrally. The zygomatic plate is flattened and nearly horizontal. It is bordered anteriorly and laterally by a crescentic ridge extending from anterior to P⁴ to the lateral edge of the zygoma. This configuration resembles that of *Cricetops*, an Asian cricetid, and a dipodoid such as *Zapus* more closely than that of a North American murid such as *Eumys*. This suggests that in *Pappocricetodon* the superficial and lateral branches of the masseter muscle were incompletely differentiated as in dipodoids (Klingener, 1964). The posterior part of the incisive foramen, preserved in three of the four specimens, terminates anterior to P⁴ and posterior to the anterior side of the ventral zygomatic root. The premaxillary-maxillary suture extends obliquely back and down to intersect the lateral side of the incisive foramen. The foramen appears to be relatively wider posteriorly than in *Eumys*. The anterior edge of the maxillary-palatine suture is approximately in line with the juncture of M¹ and M².

One of the interesting features of the four maxillary fragments is evidence on the dental formula of *Pappocricetodon*, unknown in the previously described species of the genus (Fig. 3). M¹ and M² each have three alveoli, one for a large lingual root and two for smaller buccal roots. These alveoli show that the anterobuccal root of M¹ protrudes anteriorly more than does the corresponding root of M². On all maxillae there is a small circular alveolus just anterior to the anterobuccal alveolus of M¹, indicating that a small tooth, P⁴ or dP⁴, occurred in front of M¹.

The anterior alveolar foramen (terminology follows Wahlert, 1974) pierces the maxilla in line with the posterior margin of the ventral zygomatic root. Behind it are nutrient foramina. The larger sphenopalatine foramen is at the anterior edge of the maxillary-palatine suture and above the intersection of M¹ and M².

Six incomplete lower jaws are known, of which three have teeth (V 11018.309; V 11018.310; V 11018.311). The horizontal ramus of the mandible is sturdy and the diastema is short (Fig. 4). The

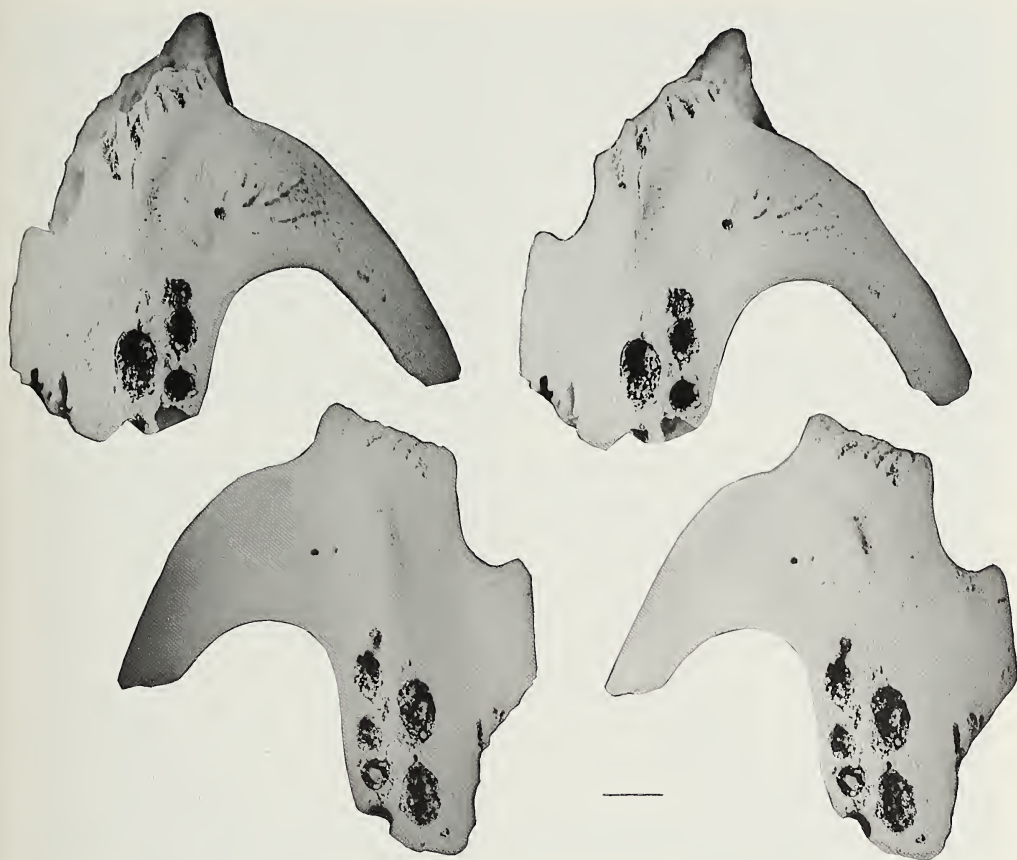


Fig. 3.—Ventral view of edentulous maxillae of *Pappocricetodon antiquus*, stereo views. Above, left maxilla, IVPP V 11018.606, showing alveoli of P⁴ (or dP⁴) and M¹. Below, right maxilla, IVPP V 11018.604, showing alveoli of P⁴ (or dP⁴), M¹, and M². Scale bar equals 1 mm.

mental foramen is anterior to M₁ and slightly above middepth of the jaw. The masseteric fossa extends forward to below M₂. Distinct upper and lower ridges form boundaries of the fossa, intersect anteriorly, and extend as a distinct ridge to below M₁. The jaw is sciurognathous.

A complete cheek tooth series is not yet known. In addition to indications from the alveoli for presence of P⁴ (or dP⁴), further evidence for the presence of a tooth anterior to M¹ comes from V 11018.90, M¹ which has a small wear facet on its anterior side. Thus, the dental formula of *Pappocricetodon antiquus* was $\frac{1.0.1.3}{1.0.0.3}$, occurring only in this genus among the Cricetidae.

The lower incisor, compressed transversely and long oval-shaped in cross section, extends into the ascending ramus. Enamel extends up to about one third of the lateral side but barely curves onto the medial side. The enamel surface has fine longitudinal ridges as in *P. rencunensis* and *P. schaubi*. Scanning electron microscope examination of the enamel of the lower incisor by Prof. Wighart von Koenigswald (letter, 17 December 1993) produced the following results (Fig. 5): "The enamel is fairly thin and has some external ridges. As normal in rodents the Portio interna (PI) and the Portio externa (PE) are well distinguishable. The PE holds only 1% of the enamel thickness. It is formed by radial enamel and the outer ridges are exclusively formed by a thickening of the PE. The interprismatic matrix is at an angle toward the prisms and anastomoses between them. The PI is built of transversely oriented uniserial Hunter-Schreger-Bands (HSB), which are vertical to the enamel dentine junction (EDJ) in a longitudinal section. In the transverse section the prisms decussate at almost right angles. The interprismatic matrix (IPM) is parallel to the prisms."

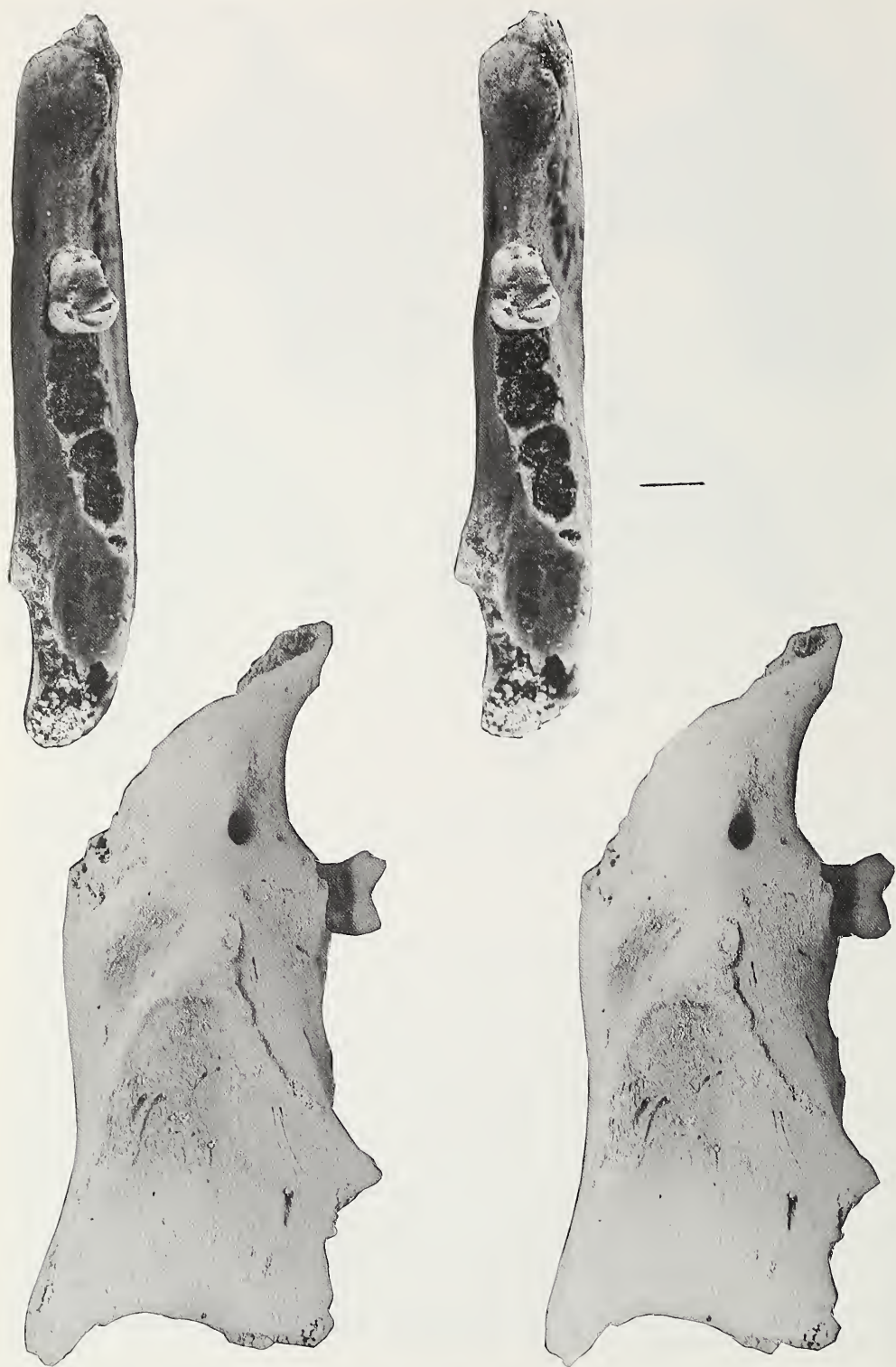


Fig. 4.—Left mandible of *Pappocricetodon antiquus*, with M_1 , IVPP V 11018.310, stereo views. Above, occlusal view showing M_1 ; below, lateral view. Scale bar equals 1 mm.

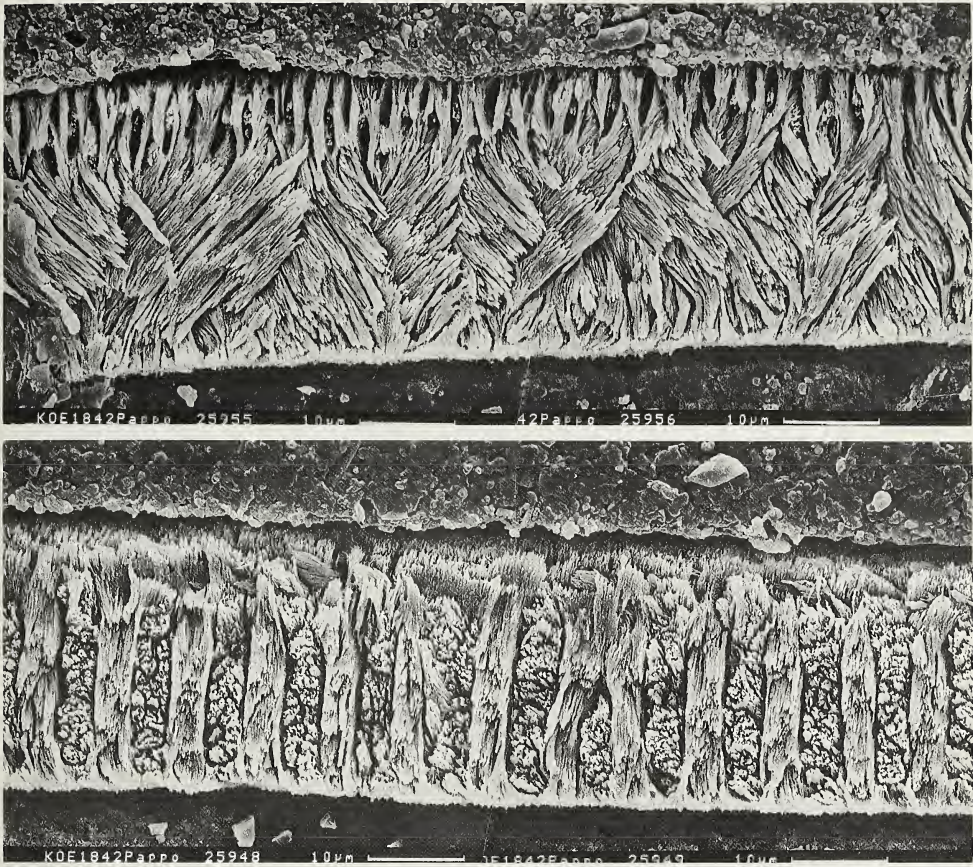


Fig. 5.—Detail of uniserial incisor enamel of *Pappocricetodon antiquus*, IVPP V 11018.611. Above, transverse section; below, longitudinal section.

The cheek teeth are brachydont and have slightly elongate cusps and weak lophs (Fig. 6). M^1 is trapezoidal in occlusal view, the buccal wall slightly longer than the lingual. Its anterior lobe is small with an anterocone that is usually distinct but small. An anterior cingulum extends from the anterocone to in front of the protocone. The protocone is bulbous, and rarely has a weak crest on the posterobuccal side (11/143). As in *P. rencunensis* and *P. schaubi* it extends slightly more buccad than the hypocone. Usually the protoloph is long (128/141) and reaches the anterocone (121/141), but in few specimens it is short and free (13/141). The protoconule on the protoloph ranges from moderate (87/143) to indistinct (56/143). Paracone and metacone are elongate transversely and subequal. The lingual crest from the paracone is weak (119/143) or absent (24/143); if present it intersects the protoloph near the protoconule (90/143) to form a complete protoloph I, or the anterior end of the mure (29/143). There is no trace of a protoloph II. The metaloph is complete and joins the mure near the hypocone. The hypocone is crescentic. Its anterior arm tapers to form the mure, which is usually long and extends far forward, variably meeting the protoloph (39/143), the lingual crest from the paracone (38/143), or the buccal side of the protocone (21/143); it may also end freely (35/143). Occasionally (6/143) it is short and joins the posterior side of the protocone. In V 11018.38, V 11018.40, V 11018.72, and V 11018.127 the mure forks into two branches: one reaches to the protocone and the other to protoloph I to enclose a small basin. The mesoloph is less well-developed than in *P. rencunensis* and *P. schaubi*, is usually short (107/143), or even absent (11/143). It is usually transverse and from medial in position to closer to the metaloph. In V 11018.38 it is oblique and extends from the intersection of the metaloph and the mure. The mesostyle is usually distinct. In some M^1 (56/135) the mesostyle has a lingual crest. The long mesoloph may be formed by a crest from the mesostyle and the short mesoloph. The mesocone is rarely present (7/143). The anterostyle may be distinct (65/139) or indistinct (74/139) and in some M^1 (25/65) it joins the protoloph. The posteroloph reaches the metacone.

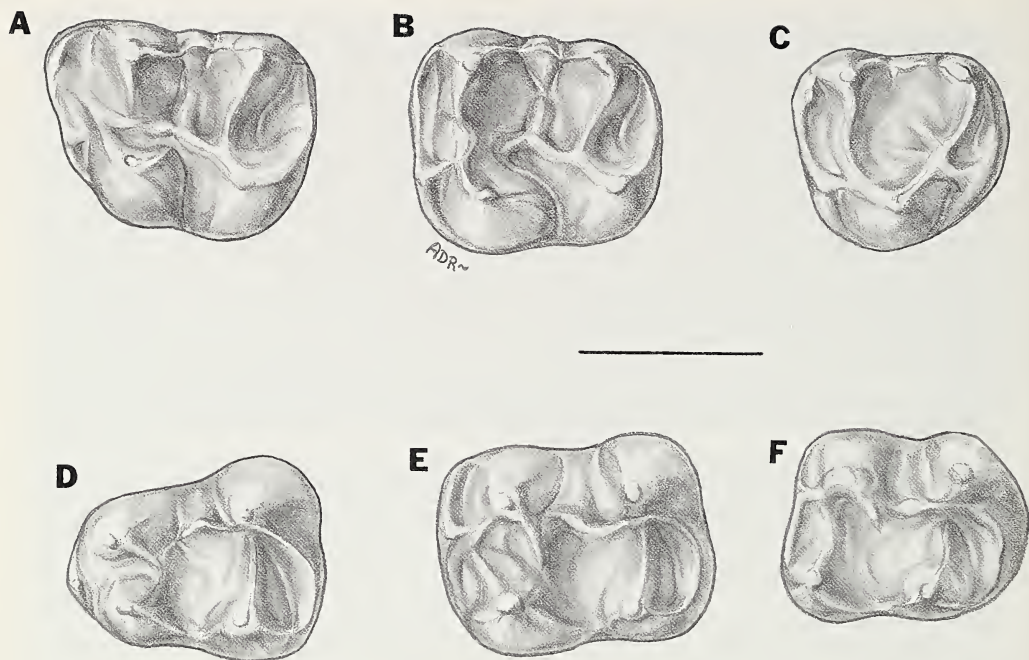


Fig. 6.—Cheek teeth of *Pappocricetodon antiquus*. A. Left M¹, holotype, IVPP V 11018.1; B. left M², IVPP V 11018.147; C. left M³, IVPP V 11018.296; D. right M₁, IVPP V 11018.419; E. right M₂, IVPP V 11018.555; F. right M₃, IVPP V 11018.590.

M² is rectangular in occlusal view, slightly longer than wide. The anterior cingulum crosses the anterior wall and joins the paracone buccally. It has a thickened anterostyle anterior to the protocone that becomes a small bridge following wear. As in M¹ the protocone is usually bulbous and rarely (23/143) has a weak crest on its posterobuccal corner. Protoloph I is complete (137/141), and appears to be formed by contributions from the protocone and the paracone. In about half of the specimens of M² (60/141), the intersection of the two crests can be seen. In some M² the crest from the protocone meets the paracone and leaves a free crest from the paracone anterior (4/141) or posterior (9/141) to it. In V 11018.189, V 11018.240, V 11018.273, and V 11018.277, for example, protoloph I is incomplete because the two crests do not intersect. The mesostyle is usually present (105/140) and has a lingual crest extending toward the mesoloph. The mesoloph may be absent (16/140), short (33/140), or of midlength (69/140). It may be forked (3/102) or double (26/102), with the anterior arm shorter than the posterior. The long mesoloph of some specimens (22/140) appears to be formed by the lingual mesostyle crest joining the short mesoloph. The mure is long, its anterior end usually turning lingually to the buccal side of the protocone (78/143); it may extend to protoloph I (16/143) or end in the valley (25/143). Occasionally it is short, reaching the posterior side of the protocone (3/143). A weak entostyle or crest is sometimes present (51/143), very rarely forming a lingual cingulum that joins the anterior cingulum (7/143). In some M² (21/143) the posterobuccal crest of the protocone may meet the mure to separate the lingual valley into open lingual and closed buccal parts.

M³, the smallest of the upper molars, varies considerably, especially in talon length and cusp development. The anterior cingulum, paracone, protoloph I, and protocone are well-developed. In some M³ (6/21), the anterior cingulum wraps around the lingual side of the protocone. The talon is not as reduced as in *P. rencunensis* and *P. schaubi*. The mesostyle is usually distinct but weak (16/21) and the mesoloph varies from weak (9/21) to absent (12/21). In the trigon basin there may be a longitudinal crest (9/21). The metacone varies from cusped to crescentic. The hypocone is less buccal than in *P. rencunensis* and *P. schaubi*. The metaloph is shorter than the protoloph I and usually complete (17/21), enclosing a small basin with the posterior cingulum. The lingual valley is shallower than in *P. rencunensis* and *P. schaubi*.

Of the three lower molars, M₂ is the largest. M₁ has a narrow trigonid as in *P. rencunensis*. Protoconid,

metaconid, hypoconid, and entoconid are similar in size and height, with buccal and lingual cusps aligned transversely. The metaconids are cusped. Most protoconids (89/113) are cusped, some are crescentic (24/113). Metalophid II is usually complete (94/113), formed by the posterior arm of the protoconid (81/113) or joined by a weak crest from the metaconid (13/113). Rarely it is incomplete (17/113) or absent (2/113). The anteroconid is a distinct cuspule that varies from rounded to elongated transversely (105/110). It is more weakly developed than in *P. rencunensis* and *P. schaubi*, usually is low and isolated (89/105) and lacks a distinct cingulum (61/105), has a weak cingulum (one lingual or buccal in 22/105), or has lingual and buccal cingula (18/105). It may be connected with the protoconid (12/105) or the metaconid (4/105). The mesostylid is distinct; it may be isolated (75/110), join the metaconid (31/110), or join both metaconid and entoconid (4/110). The mesolophid is less well-developed and may be very short (49/113), of medium length (31/113), or even absent (29/113). Rarely is it long (4/113). The mesoconid is more weakly developed than in *P. rencunensis* and *P. schaubi*, and either distinct (73/113) or absent (40/113). The ectolophid is usually complete (95/113) and straight (85/95). A few are curved (10/95), in which case the mesoconid is oblique, the anterior arm of the ectolophid is not in line with the posterior arm and is usually more weakly developed. In a few M_1 the ectolophid is incomplete and interrupted in front of the mesoconid (11/113), behind it (4/113), or is completely absent (3/113). In the latter case, the mesoconid is isolated. The hypolophid is usually complete (110/113). It differs from that in *P. rencunensis* and *P. schaubi* in being transverse and joining the hypoconid (93/113), or ending freely (3/113). In some M_1 it extends posteriorly to the posterolophid (6/113) or meets the anterior arm of the hypoconid (11/113). The posterolophid rarely has a buccal part (11/113). Although the hypoconulid is usually absent (96/113), in some it is prominent (17/113) and ends freely (3/113). In V 11018.396 the hypoconid also has a free posterior arm.

The M_2 is nearly rectangular in occlusal outline. As in M_1 the four main cusps are subequal. The lingual cusps are slightly elongate transversely and aligned with the buccal cusps. The protoconid is usually crescentic, as in *P. schaubi* but unlike *P. rencunensis*. The anteroconid is a swelling lateral to the midline on the anterior cingulum. After wear it forms a bridge joining the protolophid near its intersection with the metalophid (137/149). The metalophid connects with the protolophid (120/150), the protoconid (3/150), or the anteroconid (2/150) to form a complete metalophid I (125/150). Occasionally it is incomplete and has a free buccal end (25/150) and leaves the trigonid basin open anteriorly. Metalophid II, formed by the posterior arm of the protoconid, meets the metaconid to close the trigonid basin (89/150), or is free, leaving the trigonid basin incompletely open (61/150). Metalophid II is no greater than medium length and never reaches the lingual margin of M_2 . The mesostylid is distinct (121/149) and variable, being isolated (98/149), connecting with the metaconid (25/149), the entoconid (1/149), or both (6/149). The mesolophid is either shorter than metalophid II (93/151) or absent (57/151). In one specimen, V 11018.461, it is double. The mesoconid is oblique or transverse in orientation (70/150). Although the ectolophid is usually complete (119/150), it varies from straight (69/150) to Z-shaped (50/150). In the latter case, the ectolophid is separated by the oblique mesoconid into an anterior part that is slightly more external and lower than the posterior part. In the few specimens in which the ectolophid is incomplete, the anterior part is very low or absent (24/150) or the posterior part is very low (2/150). In five M_2 (V 11018.449, V 11018.453, V 11018.491, V 11018.498, and especially V 11018.560) anterior and posterior parts of the ectolophid are almost absent and the mesoconid is isolated and elongate transversely. The ectomesolophid is absent (122/150) or weak (28/150). As in M_1 the hypolophid is usually complete (147/150) and transverse, joining the hypoconid (95/150) or the posterior arm of the hypoconid (4/150). In some M_2 (48/150), the hypolophid meets the anterior arm of the hypoconid. The hypoconulid is usually absent (136/150). In one specimen (V 11018.467), the hypoconulid ends freely.

M_3 is a little smaller than M_1 and M_2 . The trigonid is similar to that of M_2 . The posterior arm of the protoconid is usually free (21/30). It is variable in length, midlength (13/30), short (12/30), or long (2/30). Rarely it is absent (3/30). The mesostylid is either present (14/30) or absent (16/30). The mesolophid is absent (27/30) or very weak and short (3/30). The mesoconid is absent (10/30) or variably present (20/30) and shaped as in M_2 . The ectolophid is variable as in M_2 . Unlike *P. rencunensis* and *P. schaubi*, the ectomesolophid is absent (25/30) or very weak (5/30). The hypolophid is shorter than in M_2 and usually meets the anterior arm of the hypoconid (17/30). However, in some M_3 the hypolophid joins the hypoconid (5/30), the posterolophid (5/30), or is free (3/30).

Comparisons: *Pappocricetodon antiquus* resembles the two other described species of the genus, *P. rencunensis* and *P. schaubi*, and differs from other cricetids in having relatively less enlarged M^1 and M_1 ; M^1 with a smaller anterior lobe and anterocone, protoloph I present but protoloph II absent, long protoloph usually joining anterocone; M_1 with short and narrow trigonid and small anteroconid; M_3 less reduced.

Pappocricetodon antiquus is smaller than *P. rencunensis* and *P. schaubi* (Table 1). It also differs from these species in having upper molars with a bulbous protocone and a less well-developed mesoloph;

Table 1.—Measurements (in mm) of *Pappocricetodon antiquus*.

		<i>n</i>	O.R.	\bar{x}	<i>s</i>	C.V.
M ¹	Lb	62	1.2–1.55	1.38	0.08	5.8
	Li	62	1.05–1.48	1.24	0.08	6.45
	W	62	0.95–1.25	1.10	0.07	6.36
M ²	L	60	1.15–1.55	1.31	0.07	5.42
	W	60	1.0–1.35	1.13	0.06	5.13
M ³	L	18	0.92–1.15	1.09	0.08	7.61
	W	18	0.87–1.1	1.03	0.06	6.21
M ₁	L	54	1.1–1.4	1.26	0.06	4.76
	W	54	0.8–1.05	0.94	0.05	5.32
M ₂	L	70	1.15–1.45	1.34	0.07	5.22
	W	70	0.9–1.2	1.05	0.07	6.67
M ₃	L	29	1.05–1.4	1.24	0.09	7.26
	W	29	0.87–1.15	1.02	0.06	5.88

M¹ less enlarged (M¹ length/M² length in *P. antiquus*, 1.05; in *P. rencunensis*, 1.12; in *P. schaubi*, 1.18), with a smaller anterior lobe and anterocone, resulting in the relatively less elongated buccal side; M¹⁻² with a long mure and a long, oblique lingual valley; M³ less reduced with a more distinct metacone, an indistinct, less buccal hypocone, and a shallower lingual valley; lower molars lacking ectomesolophid, having a rather transverse hypolophid that joins the hypoconid or posterolophid; M₁ less enlarged and having a less developed anteroconid (M₁ length/M₂ length in *P. antiquus*, 0.94; in *P. rencunensis*, 0.95; in *P. schaubi*, 0.98); M₃ less reduced. Except for the less distinct hypocone of M³, the features mentioned above are primitive.

The incisor enamel of *P. antiquus* demonstrates an early stage in formation of the uniserial type, which is characteristic of myomorphs (W. von Koenigswald, letter, 17 December 1993): "Compared to modern cricetids two primitive characters are found in *Pappocricetodon*. The orientation of the Hunter-Schreger-Bands (HSB) is vertical toward the enamel dentine junction (EDJ), and the interprismatic matrix (IPM) is parallel to the prisms of the HSB. In modern cricetids the HSB are inclined toward the occlusal surface and the IPM is (in lower incisors) oriented at right angles to the prisms in the third direction. The schmelzmuster of *Pappocricetodon* is more derived than in any paramyid or ischyromyid because of the uniserial HSB but primitive compared to modern cricetids."

Relationships: *Pappocricetodon* was originally described as a new genus of cricetid based on isolated teeth (Tong, 1992). No mention was made by Tong of the dental formula of this cricetid. As described above, *Pappocricetodon antiquus* is known to have a tiny P⁴ (or dP⁴). Reexamination of *P. rencunensis* and *P. schaubi* has shown that two M¹ of *P. rencunensis* (IVPP V 8928.6 and V 8928.20) have an anterior wear facet similar to that found in *P. antiquus*, indicating presence of a tooth anterior to M¹. Thus, not only *P. antiquus* but also *P. rencunensis* had P⁴ (or dP⁴) and the dental formula of *Pappocricetodon* appears to have been $\frac{1.0.1-0.3}{1.0.0.3-}$. The rudimentary P⁴ (or dP⁴) might have been shed during life.

One of the characters differentiating muroids from dipodoids is absence of P⁴ in the former. Because *Pappocricetodon* has P⁴ (or dP⁴), it could be asked whether or not *Pappocricetodon* is correctly assigned to the Muroidea. A basically similar molar pattern in primitive muroids (Cricetidae) and dipodoids supports the concept of a monophyletic origin of the Myomorpha (Wilson, 1949a, 1949b; Lindsay, 1968, 1977; Martin, 1980; Vianey-Liaud, 1985). The similarity is such that at least one genus, *Simimys*, has been transferred back and forth several times between these two myomorph superfamilies. Clearly, the primitive condition for the myomorphs must include P⁴. P⁴ of *Pappocricetodon* is very reduced. More important than its presence as a primitive feature are derived dental characters shared by *Pappocricetodon* and other cricetids but absent in dipodoids. These include: 1) M¹ has a distinct anterior lobe and anterocone; and 2) the anteroconid of M₁ is transversely elongate and has a cingulum. *Pappocricetodon* has a large, rounded infraorbital foramen, as in dipodoids and some other cricetids such as *Cricetops*, but lacks a neurovascular canal, which is a derived feature of dipodoids. Thus, derived dental features of *Pappocricetodon*, especially in the structure of the first molars, support its reference to the Cricetidae and the most primitive known genus of the family, close to the separation of muroids and dipodoids. The dipodoids are differently derived, retaining the primitive P⁴ and rounded infraorbital foramen, but developing a protective bony septum to form a neurovascular canal.

ORIGIN OF THE CRICETIDAE

Now that *Pappocricetodon* has been recognized as the earliest and most primitive known member of the family Cricetidae, hypotheses on the paleogeographic and phylogenetic roots of this family, long discussed (numerous papers from Schaub, 1925, through Tong, 1992), should be further tested. Characters of *Pappocricetodon* important in this connection are: 1. hystricomorphous-sciurognathous zygomasseteric structure; 2. anterior part of zygomatic plate nearly horizontal; 3. P^4 (or dP^4) present; 4. upper molars with bulbous protocone; 5. mesoloph(id) short; 6. metaloph contacts anterior arm of hypocone; 7. M^1 and M_1 not enlarged; 8. M^1 with small anterior lobe and anterocone; 9. protoloph I weak on M^1 ; 10. protoloph II absent; 11. protoloph short and free buccally on M^1 ; 12. mure free on M^{1-2} ; 13. lingual valley long and oblique on M^{1-2} ; 14. M^3 and M_3 slightly reduced; 15. M^3 with distinct metacone; 16. hypocone distinct, lingually located on M^3 ; 17. posteroloph complete on M^3 ; 18. M_1 with narrow trigonid and small anteroconid; 19. ectolophid absent or incomplete; 20. mesoconid oblique or transverse; 21. transverse hypolophid joins posterior arm of hypoconid; 22. incisor enamel uniserial.

Paleogeographically, the origins of the cricetids and other myomorphs can surely be sought in the Holarctic. In support of this premise is, of course, the occurrence of *Pappocricetodon* in the middle to late Eocene of Asia. To this can be added presence of a myomorph (Dawson et al., 1990) and a ?zapodid (Emry and Korth, 1989) in the early middle Eocene of North America, of *Simimys*, certainly a myomorph and probably a dipodoid, in the later Eocene of North America (Wilson, 1949a; Lindsay, 1977; Emry, 1981), and of some diversity of cricetids in the Chadronian and equivalents of North America and Eurasia. The family is not known from Africa until the Miocene and from South America until the Pliocene.

The Asian rodent record prior to the appearance of *Pappocricetodon* includes the families Alagomyidae in the earliest Eocene of Mongolia and Paramyidae in the middle Eocene of Nei Mongol. (Two species of the Eocene genus *Zelomys* were described as members of the family Sciuravidae by Wang and Li, 1990, but this assignment is still equivocal). Alagomyids and paramyids are generally primitive rodents. Alagomyids lack a hypocone on the upper molars. Paramyids have upper molars with usually well-developed conules, weak lophs from paracone and metacone converging toward the protocone to form a fairly well-marked trigon, and usually only a trace of a hypocone. In both families the lower molars have a pronounced basin. Neither has derived characters suggestive of close relationships with myomorphs. Also present in Asia were several families of the superfamily Ctenodactyloidea, first known from the early Eocene, which have been proposed as myomorph relatives (Lindsay, 1977; Flynn et al., 1985; Vianey-Liaud, 1985; Wang and Meng, 1986). Ctenodactyloids include the protrogomorphous early Eocene *Cocomys* (Cocomyidae) and hystricomorphous middle Eocene *Birbalomys* (Chapattimyidae), *Yuomys* (Yuomyidae), and *Tamquammys* (Tamquammyidae). Among them *Cocomys* and *Tamquammys* are similar to the cricetids in some primitive features such as having upper molars with a free buccal end of the protoloph and some development of a hypocone. Differences between them and cricetids are, however, more prominent: in the ctenodactyloids the cheek teeth increase in size from first to third molars; the upper molars are wider than long; the metaloph extends toward the protocone, forming a trigon similar to that of paramyids; a metaconule is present; the lower molars have a large, distinct hy-

poconulid; and the incisor enamel is pauciserial-multiserial or multiserial. To date no evidence has been found in derived characters to connect *Cocomys* or other ctenodactyloids to even the primitive cricetid *Pappocricetodon antiquus*.

European Eocene rodents are paramyids, chapattimyids (Pelaiez-Campomanes and Lopez Martinez, 1993), glirids, and theridomorphs. Characters separating paramyids and chapattimyids from cricetids are mentioned above. Glirids are clearly related to the paramyid microparamyines (Hartenberger, 1971). The most primitive theridomorphs, members of the family Pseudosciuridae, occur first in the middle Eocene. These rodents are hystricomorphous and develop uniserial enamel. P³ is absent, the upper molars have a well-developed hypocone, the mure is oblique and separated into anterior and posterior parts. A prominent feature is large P⁴ and P₄, which are never reduced. Even primitive theridomorphs differ from cricetids in having very well-developed conules, transversely-oriented main cusps on upper and lower molars, and only a rudimentary lingual valley. These differences from cricetids indicate no close affinity between these two groups.

North American early and middle Eocene rodents include paramyids, cylindrodontids, sciuravids, and some probable myomorphs. As mentioned above, paramyids show no tendency toward developing lophate teeth with well-developed hypocone and hypolophid that would be expected in relatives of the cricetids. Cylindrodontids do have a well-developed hypolophid, but their upper molars remain on a basic paramyid level of development throughout the Eocene.

The North American rodent family that stands out in dental morphology to have important features shared with the cricetids remains the Sciuravidae (Wilson, 1949b). Sciuravids are basically primitive rodents, combining a dental formula of $\frac{1,0,2,3}{1,0,1,3}$, protrogomorphous/sciuromorphous zygomaseteric structure, pauciserial incisor enamel, and brachyodont cheek teeth. In molar morphology, however, some sciuravids possess derived characters shared with early myomorphs including the primitive cricetid *Pappocricetodon* and the primitive ?zapodid *Elymys*. In the upper molars conules are reduced; protocone and hypocone are subequal and separated lingually by a pronounced valley; protoloph and metaloph are oblique, extending into the valley anterior to the corresponding para- and metacone. This last character is especially strong in *Sciuravus nitidus*, *S. altidens*, and *S. powayensis*. In *S. bridgeri* the valley between protocone and hypocone is crossed by a low crest from each cusp (Dawson, 1968:350–351). In the lower molars of *Sciuravus* the cusps are set obliquely, with lingual cusps anterior to the corresponding buccal cusps, the ectolophid is complete, the hypolophid is well-developed and the entoconid is separate from the posterolophid. There is a tendency among sciuravids toward reduction of the premolars, seen most markedly in *Sciuravus? rarus* (Wilson, 1938), AMNH 12118 (Dawson, 1962), and *Pauromys*. The Sciuravidae are here considered to be the sister group of the myomorphs (Fig. 7).

Two early middle Eocene North American genera are probably myomorphs. *Armitomys tullbergi*, the oldest known rodent with a hystricomorphous zygomaseteric structure, has incisor enamel that is transitional from pauciserial to uniserial. It seems to be a primitive myomorph but is probably not a member of the Dipodoidea (Dawson et al., 1990) because it lacks the derived neurovascular canal characteristic of that superfamily. It shares with *P. antiquus* some features, such as M¹–M² longer than wide, mesostyle present, low lophs, hypocone subequal to protocone, and bipartite metaloph. It is more primitive than *P. antiquus* in some other features including the presence of P³, probably well-developed P⁴, and

to support the affinities of *Nonomys* with the muroids (Emry, 1981), the phylogenetic importance of the neurovascular canal is here emphasized and this genus is regarded as a dipodoid.

PALEOGENE CRICETIDS IN ASIA

In the Paleogene of Asia cricetids are represented by eighteen species distributed among four genera: *Pappocricetodon* Tong, 1992 (Middle to Late Eocene of Henan, Shanxi, and Jiangsu provinces, China); *Eucricetodon* Thaler, 1966 (Early to Late Oligocene of Nei Mongol, Gansu, and Yunnan of China, Mongolia and Kazakhstan); *Cricetops* Matthew and Granger, 1923 (Middle Oligocene of Nei Mongol of China, Mongolia and Kazakhstan); and *Selenomys* Matthew and Granger, 1923 (Middle Oligocene of Nei Mongol of China and Mongolia). (Note: *Aksyiromys* and *Ulkenulastomys*, known from one tooth each, were cited as "Myomorpha, family indet." by Shevyreva, 1984. Whatever their affinities, they are apparently not cricetids and accordingly are not considered here.)

Pappocricetodon, the most primitive cricetid, includes three species: *P. rencunensis* Tong, 1992, *P. schaubi* (Zdansky, 1930), and *P. antiquus*, described above, now the earliest and most primitive member of this genus. In most features *P. antiquus* is more primitive than the other two species, but it has a more reduced hypocone on M^3 than *P. rencunensis* and *P. schaubi*, and thus appears to be a sister group to the two latter.

Eucricetodon is represented by ten taxa in Asia: *E. asiaticus* (Matthew and Granger, 1923; Lindsay, 1978) from the Middle Oligocene of Mongolia and Kazakhstan; *E. near E. asiaticus* from the Middle Oligocene of Mongolia; *E. aff. E. asiaticus* from the Late Oligocene of Kazakhstan; *E. caducus* (Shevyreva, 1967) from the Middle Oligocene of Nei Mongol of China and Kazakhstan; *E. aff. E. caducus* from the Late Oligocene of Kazakhstan; *E. meridionalis* Wang and Meng, 1986, and *E. leptaleos* Wang and Meng, 1986, from the Early Oligocene of Yunnan, China; *E. youngi* Li and Qiu, 1980, from the Early Miocene of Qinghai, China; *Eucricetodon* sp. from the Late Oligocene of Taben Buluk, Gansu, China (Bohlin, 1946), and *Eucricetodon* sp. from the Early Oligocene of Mongolia (Janovskaja et al., 1977).

Tong (1992:6-7) considered *Eucricetodon meridionalis* to be more similar to *Pappocricetodon* than to *Eucricetodon* on the basis of the following shared features of tooth morphology: M^1 with a very small anterior lobe, a well-developed protoloph joining anterocone with protocone, and a single anterocone; small M_1 about same length as M_2 and with small anteroconid and trigonid; no free arm of hypoconulid. Tong concluded that *E. meridionalis* was more closely related to *Pappocricetodon* than to other cricetids and might be in the same evolutionary lineage as *P. rencunensis* and *P. schaubi*. However, *E. meridionalis* is here considered to be a species of *Eucricetodon* that has more primitive features than other species of *Eucricetodon*. All the similarities mentioned by Tong are primitive features. In comparison with *Pappocricetodon* and *Eucricetodon*, *E. meridionalis* shares with the latter such derived features as M^1 having an enlarged anterior lobe, a large anterocone, lacking protoloph I but having a complete protoloph II, a large anteroconid, and M_1 longer than M_3 . *E. meridionalis* is here retained in *Eucricetodon*.

Tong (1992:7) also doubted the position of *E. leptaleos* in *Eucricetodon* because he thought it had the following special characters: 1) short protoloph (=anterior arm of protocone in Tong, 1992) extending towards paracone or joining crest

from paracone (=protoloph in Tong, 1992); 2) anterocone(id) small and with a smooth posterior surface; 3) absence of a bridge from anterostyle (=caudaler anteroconussporn of Dienemann, 1987, and Tong, 1992); 4) M^3 having simple structure; 5) M_1 equal to M_2 in length; 6) weak lophs on lower molars; and 7) M_3 with a reduced talonid. Of these, 1, 2, 3, 5, and 6 are primitive features of cricetids and similar to those of *Pappocricetodon*, and 4 is variable in cricetids and probably not phylogenetically significant. Only 7 is a derived feature but it is shared by *Eucricetodon*. In fact, in *E. leptaleos* the anterior lobe of M^1 is enlarged and forms a distinct lobe, the anterocone is large, and protoloph II has begun to form, as in *Eucricetodon*. Thus, *E. leptaleos* appears to be a primitive species of *Eucricetodon*.

Pappocricetodon rencunensis and *P. schaubi* share some derived features: a long protoloph joining the anterocone on M^1 , a well-developed mesoloph, and a buccal hypocone on M^3 . These features differ from those of *Eucricetodon*, including *E. meridionalis* and *E. leptaleos*, and other later cricetids. However, among the cricetids *Eucricetodon* is closest to *Pappocricetodon*. Possibly primitive cricetids in Asia may have divided into two lineages, with *Pappocricetodon* representing a primitive group, and another lineage represented by *Eucricetodon* and other Asian cricetids, in which M^1 and M_1 are enlarged and have a large anterocone(id) and M_1 has a well-developed anterior cingulum. There remain many gaps in the history of cricetids in Asia, however, with such problems as the origin of *Cricetops* and the peculiar *Selenomys* still to be resolved.

PALEOGENE CRICETIDS IN THE HOLARCTIC

Now that the geologically oldest and morphologically most primitive cricetid rodents are known to occur in the Eocene of Asia, implications of the entirely Holarctic Paleogene stratigraphic and biogeographic record of the family should be reconsidered. *Pappocricetodon* is important in providing evidence on primitive characters of cricetids that allows a clearer understanding of character polarity among Paleogene forms. No attempt is made here to revise the family at the subfamily or any other level. Currently the infrafamilial arrangement of cricetids can conservatively be characterized as in a state of flux (contrast, for example, the familial and subfamilial associations of Martin, 1980, Ünay-Bayraktar, 1989, and Freudenthal et al., 1992).

Cricetids appeared in Europe after the Grande Coupure. Since that event cricetids (sensu lato) diversified and dispersed rapidly in Europe. Thirteen genera are recognized (Freudenthal et al., 1992) in the European Paleogene record. The earliest cricetid is *Eucricetodon atavus* from Hoogbutsel (the *Eucricetodon atavus* tooth from the pre-Grande Coupure locality Mohren 6 should be dismissed due to faunal mixing within the fissure, following the discussion in Dienemann, 1987). It resembles the Asian *E. meridionalis* in size and some aspects of tooth morphology, but is more derived in having first molars with a larger anterior lobe and anterocone(id) and more reduced third molars. The record supports the hypothesis that *Eucricetodon* migrated from eastern Asia into Europe after the Grande Coupure.

In North America, as in Europe, a major cricetid radiation occurred in the Oligocene (*Eumys* sp. described by Storer, 1988, from the Duchesneau of Saskatchewan has been referred to the Sciuravidae by Dawson, in press), from which eight cricetid genera have been reported (Martin, 1980). They have some common features, such as more or less swollen main cusps, short posteroloph and well-developed metacone on M^3 , which differ from those of Asian Paleogene cricetids,

including *Pappocricetodon* and *Eucricetodon*. The North American cricetids *Eoemys*, *Scottimus*, *Leidymys*, *Geringia*, and *Pacculus* are not referable to the Eurasian Eucricetodontinae (Tong, 1992, contra Martin, 1980). The Oligocene genera *Geringia* and *Pacculus* have a small anterocone-anteroloph that differentiates them from contemporary North American cricetids. This state has been regarded as a reduction from the *Eumys* condition. The morphology of the primitive Asian *Pappocricetodon* opens the possibility that these genera represent another immigration from Asia rather than a reduction from North American endemic rodents.

ACKNOWLEDGMENTS

This report would not have been possible without the encouragement and support of and discussions with our colleagues Chris Beard and Qi Tao, whom we thank most sincerely. We are also grateful to Wighart von Koenigswald and Jin Meng for their work on the incisor enamel of this early cricetid. Illustrations were skillfully done by Andrew D. Redline, photographs by Chris Beard and Wighart von Koenigswald. We appreciate reviews of this manuscript by Robert Emry and Everett Lindsay, whose comments helped in clarifying our results. The larger project on Paleogene fissure fillings from China is supported by grants from the National Science Foundation (DBS 9221231), the Chinese National Science Foundation (grant no. 49372070), and the M. Graham Netting and Edward O'Neil funds of Carnegie Museum of Natural History.

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MEDIOCAMPUS, A NEW STINKBUG
GENUS FROM THE DOMINICAN REPUBLIC
(INSECTA: HETEROPTERA: PENTATOMIDAE)

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ABSTRACT

A new genus, new species, in the stinkbug family Pentatomidae, *Mediocampus dominicanus* is described from the Dominican Republic. The genus is apparently related to the Antillean genera of the Pentatomini with a xiphoid metasternum, *Pharnus*, *Neopharnus*, and *Praepharnus*. It differs in that the metasternum is deeply sulcate for reception of the rostrum and the abdominal tubercle is bicarinate. These genera, especially the new genus, occupies a phylogenetic position somewhat intermediate between the Pentatomini and the Edessini.

INTRODUCTION

As a result of intensive collecting in the Dominican Republic by staff members of the Carnegie Museum, a new genus of stinkbug, herein described, was discovered. The new genus is represented by two female specimens from two localities separated by a distance of approximately 65 km. Both localities were low elevation (230 m), riparian woodland habitats. The specimens were collected at lights. The new genus appears to be related to a small group of genera known to occur primarily on the island of Cuba.

Mediocampus, new genus
(Fig. 1-3)

Type Species.—*Mediocampus dominicanus*, n. sp.

Diagnosis.—Metasternum bilaterally elevated, longitudinally, mesially sulcate for reception of rostrum; broadly notched posteriorly in apposition to basal abdominal production; projecting anteriorly as narrow elongate arm on each side of mesosternum. Mesosternum flat, narrow, with low bicarinate apical process projecting anteriorly between procoxae. Basal production of abdomen strongly sulcately excavated mesially, lateral margins of sulcus obtusely carinate; each carina projecting anteriorly into metasternal notch as subspinous production (Fig. 2). Bucculae prominently arcuate anteriorly, evanescently contiguous posteriorly. Apex of scutellum acuminate.

All femora unarmed. Tarsi three-segmented. Antennae five-segmented. Trichobothria on abdominal sternites II–VII in line with spiracles. Base of rostrum originating anterior to middle of head.

Etymology.—Latinized from Spanish *Mediocampo*, literally *medio* meaning “middle,” and *ocampo* meaning “field,” in reference to the intermediate position of the genus between the typical pentatomines and the plesiomorphic edessines.

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Submitted 11 March 1994.

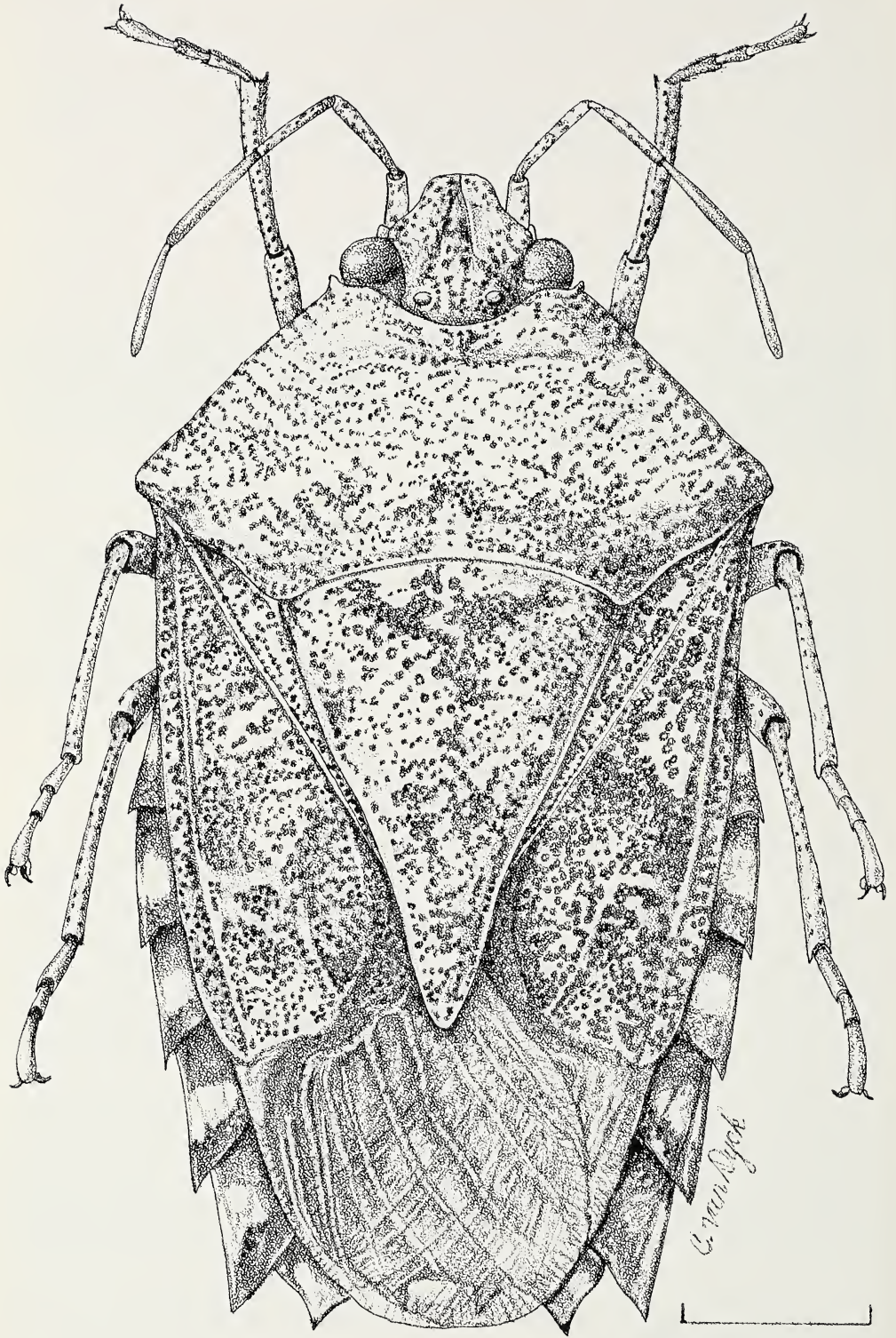


Fig. 1.—*Mediocampus dominicanus*, dorsal aspect. Bar = 2 mm.

Mediocampus dominicanus, new species

Description.—Elongate, ovate; length excluding membrane 11 mm, width across humeri 7 mm. Stramineous dorsally with fuscous yellow hemelytral coria and scutellum; dorsal and ventral surface with reddish-brown punctures irregularly distributed. Connexival segments with dark brown anterior and posterior infra-margins alternating with pale yellow meson.

Head. Length from apices of jugs to line of ocelli slightly greater than anteocular width. Jugs broadly contiguous anteriorly, lateral margins strongly sinuate. Antennal segment I shortest; II slightly longer than III; III about two-thirds length of IV; IV and V longest, subequal. Rostrum long, extending to third abdominal segment (second visible); segment II longest, slightly longer than III; segments I and IV subequal to one another and about two-thirds length of II.

Thorax. Anterolateral pronotal margin smooth, without marginal bead, sub-rectilinear in dorsal view. Humeri angular, not produced. Basal margin of pronotum arcuately concave; posterior angles not acutely produced. Scutellum proportionately long, apex extending to posterior limit of coria. Posterior margin of corium evenly arcuate; membrane infuscated. Metasternal scent gland evaporatorium maculate with spots equal in size and density to the dark punctures scattered over rest of venter. Ruga of scent gland orifice elongate, extending two-thirds distance to metapleural margin. Protibia subprismatic, meso- and metatibiae cylindrical with elongate sulcus.

Abdomen. Apices of connexiva acuminate. Lateral angles of sternite VII strongly spinosely produced. Margin separating segments III and IV effaced mesially. Spiracles large, oval.

Genitalia. First gonocoxites briefly contiguous at base, triangulum exposed medially; second gonocoxites narrow and emarginate posteriorly; eighth paratergites strongly angularly produced posteriorly; spiracles present; ninth paratergites narrowly acuminate (Fig. 3). Males unknown.

Type Specimens.—Holotype, female. Verbatim label data: "DOMINICAN REPUBLIC: Barahona. 9.2 Km NW Paraiso, confluence of Rio Nizao and Rio Coltico 18-03N 71-12W 230m 9-10 Aug 1990 J. Rawlins, S. Thompson." Deposited Carnegie Museum Natural History.

Paratype, female. (a) "DOMINICAN REPUBLIC: Pedernales. Along Rio Mulito, 13 Km N. Pedernales, 18-09N 71-46W." (b) "230m, 17 July 1992, J. Rawlins, S. Thompson, C. Young, R. Davidson. Riparian Woodland." Deposited Carnegie Museum Natural History.

DISCUSSION

The character states separating the neotropical subfamily Edessinae from the cosmopolitan Pentatominae are somewhat ambiguous. Four edessine genera, all restricted to the New World, are recognized: *Edessa* Fabricius, *Peromatus* Amyot & Serville, *Olbia* Stål, and *Pantochlora* Stål. Leston (1955) recognized the tribes Edessini and Pantochlorini within the subfamily Pentatominae. Rolston and McDonald (1979) did not acknowledge the tribal separation, but elevated the four genera to their own subfamily, Edessinae. All have a strongly-elevated metasternum which projects over the mesosternum; all have a short rostrum which extends only to the mesosternum in repose; all have the bucculae of the oral groove united behind the rostrum, and all have parandria or dorsal genital plates on the interior surface of the male pygophore. However, none of these character states is unique to the edessines, but occur singly or in combination in many pentatomines. The

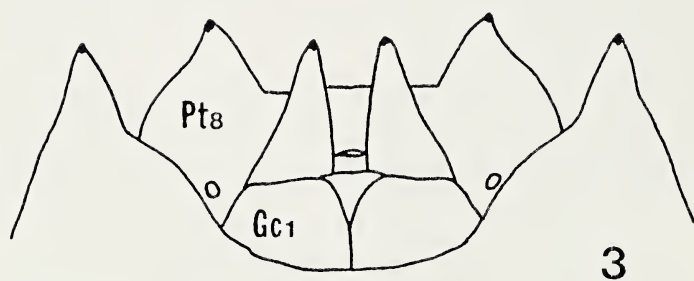
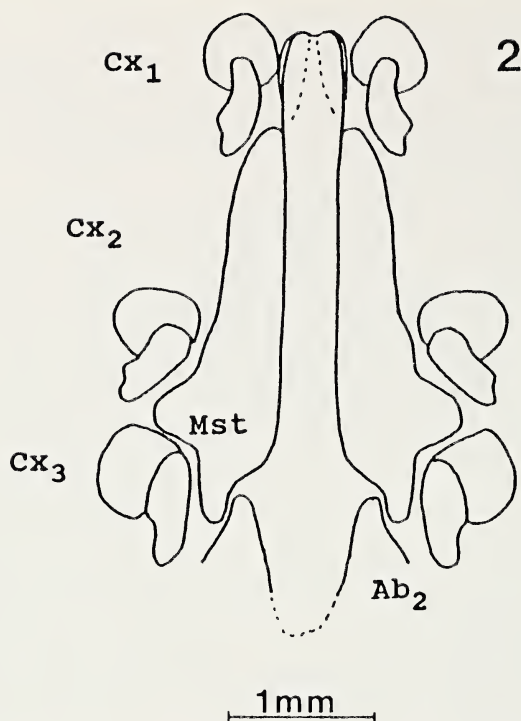


Fig. 2-3.—2. Metasternal and abdominal armature, ventral view. Cx = coxa, Mst = metasternum, Ab₂ = second abdominal segment. 3. Female terminalia. Pt₈ = eighth paratergite, Gc₁ = first gonocoxite.

genus *Piezosternum* Amyot & Serville has all of these characters but is placed in the Tessaratomidae, subfamily Oncomerinae, by Kumar (1968) because it has the additional character of the pronotum overlying the base of the scutellum. For this reason the Edessinae may be considered to be the stock derived most closely to the sister family Tessaratomidae.

Mediocampus is very "edessoid" in aspect and my first impression on seeing

these specimens was that they were a species of the large genus *Edessa*. On examining the ventral armature for the characteristic xiphoid metasternum found in all members of the latter genus, I found the xiphoid metasternum with typical long anterior arms present, but with the unusual character of a groove or sulcus mesially for the reception of the long rostrum. A similar, but even more exaggerated condition occurs in some South Pacific asopine genera, namely *Ealda* Walker and *Cantheconidea* Bergroth, but that is clearly a case of convergence and not relation. Another distinctive character is the bifid abdominal tubercle. A similarly bifid abdominal tubercle occurs in the African genera *Glypsus* Dallas and *Bathycoelia* Amyot & Serville, which otherwise bear little resemblance to the new Antillean genus.

Rolston et al. (1980) divide the Pentatomini into three sections based on the ventral armature. *Mediocampus* belongs to section 3, those having an abdominal tubercle in apposition to an elevated metasternum. In the key to this section *Mediocampus* falls out with a small group of Antillean genera which, like *Edessa*, have a xiphoid metasternum: *Pharnus* Stål, *Neopharnus* Van Duzee, and *Praepharnus* Barber and Bruner. In their description of the latter genus, Barber and Bruner (1932) considered *Praepharnus* "more closely related to *Pharnus* than to *Edessa*. . . ." *Mediocampus* appears to lie between *Praepharnus* and *Edessa*. It is similar to *Praepharnus* in size, elongate depressed form, straight anterolateral pronotal margins, and long slender rostrum. It shares with *Edessa* the long anterior arms of the metasternum and the posteriorly-united bucculae. It is unlike both genera in having the bicarinate abdominal tubercle and the sulcate metasternum. This sulcus is continuous with a sulcus on the abdominal midline, in contrast to the keeled abdominal midline in *Praepharnus*.

It is interesting to speculate that these three endemic Cuban genera, plus the new Hispaniolan genus, might be offshoots from a lineage close to the base of the edessines and pentatomines that differentiated and persisted in isolation in the Greater Antilles.

ACKNOWLEDGMENTS

I am grateful to John Rawlins for making these specimens available to me for study, and to L. H. Rolston and Pieter van Doesburg for advice on character states in the Edessinae. The habitus drawing of *Mediocampus dominicanus* was executed by Chris Van Dyke.

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REVIEW

NEW JERSEY FERNS AND FERN ALLIES. James D. Montgomery and David E. Fairbrothers. 1992. Rutgers University Press, New Brunswick, New Jersey. 293 pp. with line drawings. ISBN 0-8135-1817-2. \$45.00.

New Jersey Ferns and Fern Allies begins with a historical introduction of botanical field studies in New Jersey, especially those on pteridophytes. This subject, vast enough to warrant its own book, is substantially condensed in a one-chapter treatment.

Other prefatory chapters include "Fern Structure and Classification," "Hybrids," "Keys," and "Ecology and Distribution." These chapters discuss the terms used in the keys, how hybrids arise and some characteristics for hybrids identification, and the ecology of New Jersey, including how pteridophyte distribution is related to ecological regions in the state. The authors make these subjects understandable even for novice botanists.

This fern flora is more than just a description of all 83 species of ferns and fern allies found in the state. Specimen occurrences for each species are plotted on maps using three different-sized dots to indicate records from pre-1900, 1900–1950, and post-1950. This system reveals chronological trends for each species—whether its populations are declining, expanding, or remaining static. Although each dot represents a herbarium specimen, the authors fail to list which herbaria were consulted. This information would be useful for future floristic projects in New Jersey. Taxa apparently absent from New Jersey but found in bordering regions are mentioned in the accounts of closely related species.

Each taxonomic chapter treats a single genus, beginning with a description of the genus and a key to the species (and hybrids) found in New Jersey. Each species account provides scientific name, synonyms, common name, and a brief description of the plant, including its habitat, range, and distribution in New Jersey. Comments include chromosome number and endangered status in the state. Each distribution map is paired with an excellent line drawing by Kathleen L. John-Alder, often with a smaller closeup drawing of diagnostic characteristics. The illustrations in the genus *Ophioglossum* are reversed. For ease of reference, text and figures for most species accounts are on facing pages, which also results in a good deal of blank space.

The keys in the manual, including a vegetative key to ferns of New Jersey, are easy to use by anyone with a basic knowledge of pteridophyte terminology. It is refreshing that the authors include hybrids in the keys, instead of mentioning them only in passing as is too often the case. Thirty-two hybrids are discussed, with descriptions, illustrations, and maps of the 17 that occur most frequently.

The included checklist of all pteridophyte species and hybrids found in New Jersey will be useful to those involved in floristic studies of New Jersey and nearby states. The bibliography is excellent for anyone interested in delving deeper into the pteridophytes of eastern North America.

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INSTRUCTIONS FOR AUTHORS

ANNALS OF CARNEGIE MUSEUM consist of contributions to the earth sciences, life sciences and anthropology, in 30 by 46 picas format (127 by 195 mm or 5 by 7½ inches). Submit all manuscripts to the Office of Scientific Publications. Authors should give particular attention to scientific content, format, and general style for the ANNALS. Manuscripts that do not conform to the style of the ANNALS will be returned to the author immediately. Every manuscript will be peer reviewed by at least two outside persons. Authors will be asked to subsidize, if funds are available, any or all costs of publication (approximately \$100/page printed).

Manuscript style.—Articles should include the following items in this order: title page, abstract, text (with desired headings), acknowledgments, literature cited, tables, figure captions, and copies of illustrations. All manuscripts must be typed *double-spaced* on standard 8½ by 11 inch white bond paper, with at least one inch margins all around, and submitted *in triplicate*—an original for the editors, and two review copies. All pages should be numbered, including tables, literature cited, and the list of figure captions. Only correspondence quality or better dot matrix printouts will be accepted; draft mode is unacceptable. A fixed-space font (e.g., Courier) is preferred.

Title Page. The title, on a separate title page should be brief, include the animal or plant group involved, and appear two to three inches below the top margin. Include the authors name(s) and the affiliations of non-CMNH authors. In the case of multiple authorship indicate the address to which proofs should be sent.

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- 5) Unpublished dissertation:
SMITH, J. P. 1976. Review of Eocene mammals. Unpublished Ph.D. dissert., University of California, Berkeley, 302 pp.
- 6) Book:
WHITE, M. J. D. 1961. The Chromosomes. Methuen and Co., Ltd., London, 120 pp.
- 7) Journal articles with usual volume and issue number:
ANDERSON, W. I. 1969. Lower Mississippian condonts from northern Iowa. Journal of Paleontology, 43(4):916–928.

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VOLUME 63

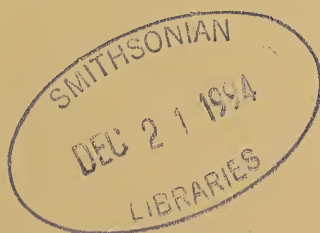
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NUMBER 4

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ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

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THE CARNEGIE
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ARCHAEOLOGY OF TRANTS, MONTSERRAT. PART 1.
FIELD METHODS AND ARTIFACT DENSITY DISTRIBUTIONS

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ABSTRACT

Different research strategies used during archaeological fieldwork in 1978-79 and 1990 at the early Ceramic Age site of Trants are compared and evaluated. Site size and the area of "major concentration" of artifacts were both underestimated by the field methods employed during initial research in 1978-79. The "collection corridor" strategy used in 1990 was an efficient and effective technique for systematic surface collection and, when combined with subsurface data from spaced test pits, it proved to be a reliable method for distinguishing artifact densities and determining site parameters. Low-density artifact distributions existing in peripheral fields were distinguished from a "most dense" area (ca 90,000 m²) demarcated by surface and subsurface artifacts, in which a "core area" (ca 50,000 m²) delineated the site's oval-shaped configuration. A ca 500 B.C. initial occupation at Trants is substantiated by the two oldest radiocarbon dates and by diagnostic pottery ascribed to the Saladoid ceramic series. Terminal radiocarbon dates (ca A.D. 330) suggest that Trants was inhabited, either continuously or intermittently, for perhaps 800 years. Trants is one of three early Ceramic Age sites on Montserrat that have yielded Saladoid ceramics. This article is the first in a series of individually numbered parts dealing with the results of archaeological field research at the Trants site.

INTRODUCTION

Trants is the largest and oldest of three confirmed early Ceramic Age sites on Montserrat. At Trants, site disturbance by historic and recent cultivation is minimal, the stratigraphic integrity of its archaeological deposits is excellent, and the preservation of its artifacts and ecofacts is superb.

The island of Montserrat is located in the Lesser Antilles, the archipelago forming the eastern border of the Caribbean Sea and demarcating the western edge of the Atlantic Ocean. These islands form an 850-km long arc from Sombrero south to Grenada (Fig. 1). North of Guadeloupe, the Lesser Antilles islands form a double arc, the Outer or Limestone Arc and Inner or Volcanic Arc. Montserrat is one of the smaller (98 km² volcanic islands on the Inner Arc of the northern Lesser Antilles. Three major mountain masses, trending north to south down the center of the island, dominate Montserrat's landscape (Fig. 2). The Trants site is situated east of the Centre Hills on the only sizeable stretch of relatively flat terrain near sea level along the windward coast (Fig. 3). The rest of this coast is marked by precipitous cliffs.

The Trants Estate, comprising the generally level terrain surrounding the Trants site, encompasses a much larger area (ca 600,000 m²) and is bounded by mountains to the west and north, the coast to the east, and a river valley to the south. Trants Estate is named for Dominick Trant, a plantation owner in the 1720s (Marion Wheeler, personal communication, 1990). Since the 1950s, this estate has been the property of the Government of Montserrat. Trants Estate no longer is a working agricultural plantation; instead it is used for pastureland and small garden plots.

Montserratians have collected Amerindian artifacts at Trants for many years.

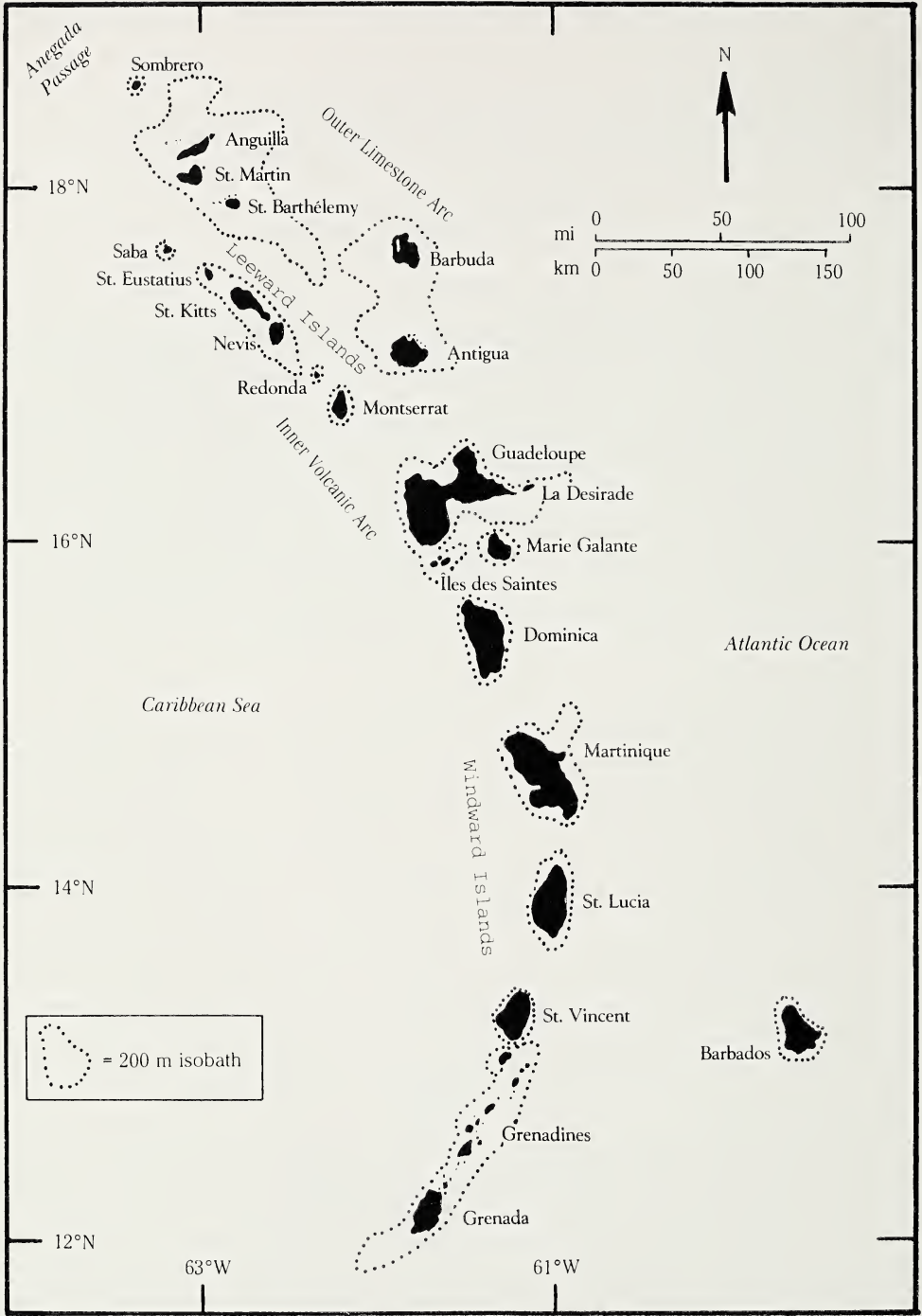


Fig. 1.—The arcuate Lesser Antilles stretch from Sombbrero to Grenada. Sombbrero lies about 100 km east of the Virgin Islands, the easternmost islands of the Greater Antilles (see Fig. 2); Grenada lies about 150 km north of the South American continent.



Fig. 2.—The Trants prehistoric site is located midway on the east coast of Montserrat in the northern Lesser Antilles.

Prehistoric beads were the focus of Harrington's (1924) brief article, the first publication to discuss artifacts from the site. The beads formed one part of a large and diverse collection of artifacts from Trants acquired by the Museum of the American Indian (MAI), Heye Foundation, from Seymour Wylde Howes, the manager of Trants Estate (Watters and Scaglione, 1994). The lithic beads and ceramics in the Howes collection were studied respectively by Watters and James B. Petersen in 1985; they re-examined the MAI materials in 1991; and in 1994 Watters examined objects from the Howes collection that the MAI had exchanged with the University Museum, University of Pennsylvania in 1932.

The first archaeological survey and excavation at Trants occurred during 1978–79, as part of Watters' (1980) dissertation research on the islands of Montserrat and Barbuda. Trants, the first site recorded in St. George's Parish, was assigned site number MS-G1. The second field season, which took place in 1990, involved additional survey and testing at Trants, included a study of Trants artifacts housed at the Montserrat National Trust Museum, and was a collaboration of the Carnegie Museum of Natural History (CMNH) and the University of Maine at Farmington (UMF). The CMNH-UMF project was jointly directed by Watters and Petersen. The Trants site was observed briefly in 1983, 1984, and 1992, during short stopovers on Montserrat made in the course of other research projects on nearby islands.

Preliminary information about the 1990 field season has been published already (Bartone and Crock, 1991; Petersen and Watters, 1991). Data from the 1978–79 project (Watters, 1980) are used in two regional studies: a report on the thin section petrography of ceramics from four northern Lesser Antilles islands (Donahue et al., 1990), and a compilation of Late Quaternary vertebrate faunas from archaeological and paleontological contexts throughout the Lesser Antilles islands (Pregill et al., 1994).



Fig. 3.—A view (looking west) from an airport tower across the Trants site toward the Centre Hills. Field 10 is the pasture in the foreground; Field 8 lies just beyond the treeline, where the cement block building is visible (indicated by the arrow).

This article is Part 1 in a series of separately numbered reports dealing with the results of the archaeological research at the Trants site. These reports focus on the 1990 fieldwork although selected articles will deal with aspects of the 1978–79 research as well. Part 2 of this series reports the vertebrate fauna recovered from three 1990 excavation units (Reitz, 1994) and combines those data with the previously published vertebrate fauna from the 1978–79 research (Steadman et al., 1984). Other parts will discuss sediment data and settlement patterns, lithic technology, paleoethnobotanical remains, and invertebrate faunas. Data derived from museum research on the S. W. Howes collection are being published as separate articles (Watters and Scaglion, 1994), to divorce those reports from the individually numbered parts of the Trants field research series.

The purposes of Part 1 in the Trants archaeology series are to: (1) compare and evaluate field methods used in 1978–79 and 1990; (2) provide data on derived artifact densities and spatial distributions; (3) interpret these data with respect to site demarcation and configuration; (4) discuss the chronological placement of the Trants site and its occupational span; (5) review the relationship of Trants to Montserrat's other six prehistoric sites; (6) and furnish the background information, about the surface samples, test pits, and excavation units, that is integral to the presentations in the forthcoming parts of this series.

FIELD METHODS

Archaeological Surveys

Field research on Montserrat in 1978–79 was conducted by the author and one field assistant. The strategy used in the survey to locate prehistoric sites involved

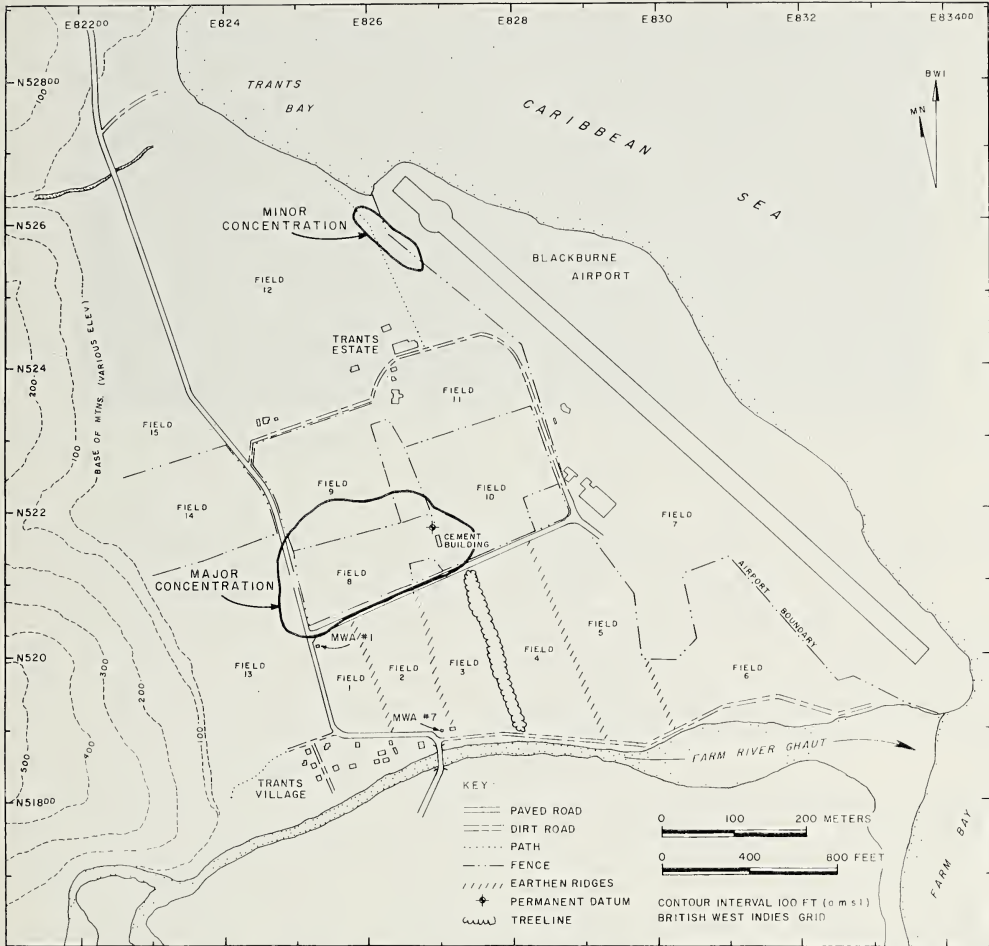


Fig. 4.—Locations of the “major” and “minor” concentrations of surface artifacts identified during initial fieldwork in 1978–79. Northing and easting based on the British West Indies (BWI) grid, which differs from the site grid (see Fig. 17).

six randomly selected, 250 m-wide cross-island transects (Watters and Scaglion, 1980). The northern part of the Trants site was discovered near the eastern terminus of Transect 28 at Trants Bay (Watters, 1980:214–215). This area, designated the “minor concentration,” was identified through surface artifacts found due west of the north end of the Blackburne Airport runway (Fig. 4). A “major concentration” of artifacts was detected subsequently in an area outside of the Transect 28 boundaries, exposed on the surface of a field planted in sea island cotton immediately north of the road to Blackburne Airport. Few surface artifacts were observed in the other fields north of the airport road, most of which were in grass and used as pasture; fields south of that road, being covered by thickets of thorny “cassie” bushes, were unobservable for the most part. At the end of the 1979 survey, the minor and major concentrations were regarded as spatially distinct sectors, perhaps representing two site components, that were separated by an intervening area of about 350 m of grassy pasture having few artifacts.

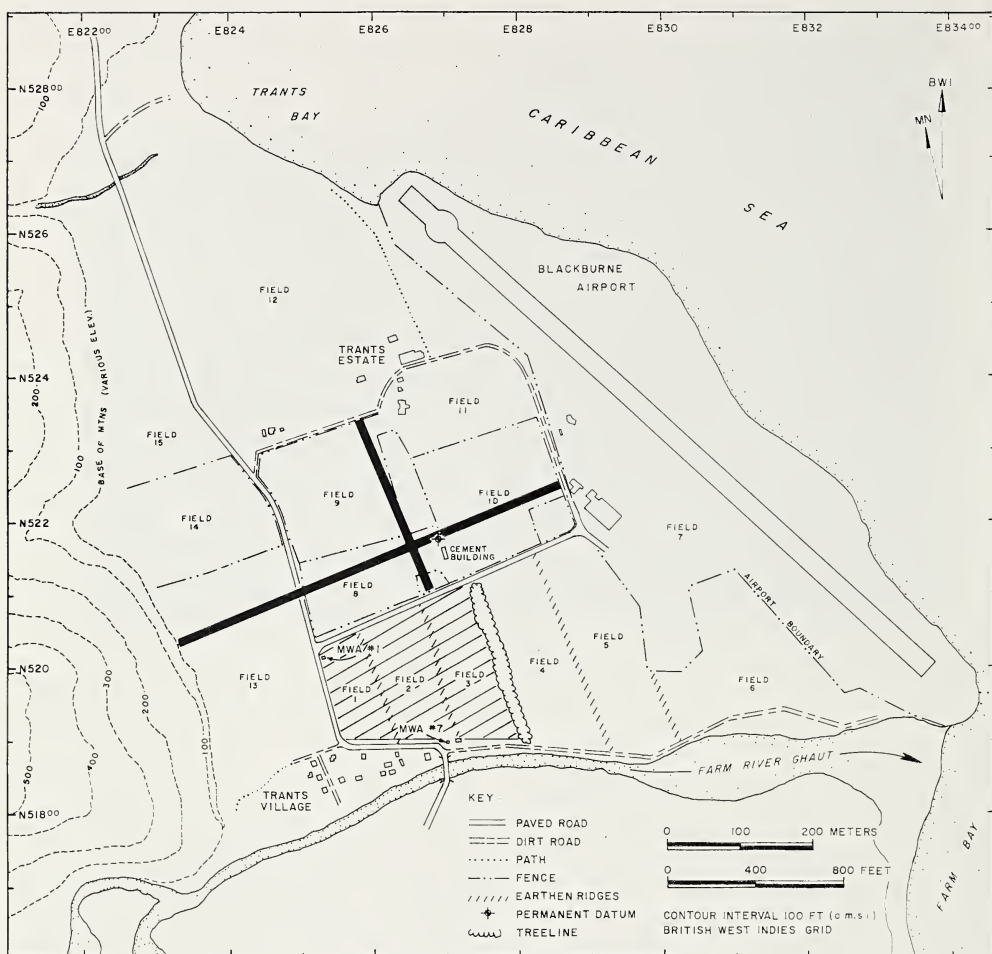


Fig. 5.—Systematic collection strategies used to obtain data on surface and subsurface artifact densities at Trants during the 1990 fieldwork. Note locations of numbered fields (BWI grid).

Based on observed surface artifacts, the total area of the Trants site, combining the major and minor concentrations, was estimated at about 42,500 m² (Watters, 1980:table 8), or 4.25 hectares.

Brief visits to Montserrat in 1983 and 1984 reconfirmed the locations of the major and minor concentrations and provided the opportunity to examine, for the first time, the fields south of the airport road from which the cassie thickets had been removed in the interim. Few artifacts were observed in these newly cleared fields.

Different strategies were used during the CMNH-UMF project in 1990. The ten-week field season involved seven people although not everyone participated for the entire project (Petersen and Watters, 1991). The primary objectives were to: (1) examine the relatively flat terrain (60 hectares) surrounding the Trants site, from the coast to the mountains, for evidence of cultural materials; (2) define more accurately the extent and boundaries of the site; and (3) determine the depths



Fig. 6.—Crew members pin flagging artifacts in a 10×10 m surface collection unit in Corridor 1.

of its cultural deposits. These goals were paramount because the Trants site was potentially threatened by two projects proposed for the adjacent Blackburne Airport: realignment of its runway, and construction of new airport buildings.

The archaeological survey area included the terrain east of the mountains to the coastline between Trants Bay and Farm Bay (Fig. 5). The southern border was Farm River Ghaut (ghaut is a term used locally to signify a steep-sided valley). To manage the archaeological survey, the terrain was designated as Fields 1 through 15, using already existing roads, fencelines, earthen ridges, and wind-breaks as the boundaries of the subdivisions.

Surface collections were made during the very dry month of September and in early October when the seasonal rains were just starting. The exposure of the ground surface by the die-back of vegetation enabled excellent observation of surface artifacts.

Three systematic surface collection strategies were used in Fields 1, 2, and 3 south of the airport road (Fig. 5). Surface artifacts in all three fields were pin flagged and counted, but the percentages shot-in by transit and collected varied among the three fields. In general, artifacts were sparsely distributed in these fields.

A similar systematic surface collection strategy initially was used in the southeast sector of Field 8, immediately west of the cement block building, in an area coinciding with part of the previously defined major concentration. The high density of artifacts in Field 8, in comparison to their scarcity in Fields 1 through 3, required a change in strategy for surface collecting. A more efficient sampling strategy was needed to maximize the systematic survey coverage and to facilitate the comparison of spatial distributions of artifacts.

A “collection corridor” technique was devised to sample the surface artifacts. It involved a linear arrangement of adjacent 10×10 m squares in which surface artifacts were flagged (Fig. 6) and collected but not shot-in by transit. Corridor 1, the corridor spanning the terrain (Fig. 5) from the mountains to the present airport boundary, traversed Fields 13, 8, and 10 from west to east (Fig. 7). Corridor 2 traversed Fields 8 and 9 from south to north between the airport road and the estate road (Fig. 5).

Data for two categories of artifacts, pottery and lithics, from the 56 collection



Fig. 7.—A fully flagged 10×10 m surface collection unit in Corridor 1 in Field 8.

squares in Corridor 1 are included in this paper. When plotted by 10×10 m surface squares, counts for both artifact categories have somewhat narrow distributions, with a decided peak consistently occurring toward the east side of Field 8 (Fig. 8). Field 13 and much of Field 10 yielded many fewer artifacts. When Corridor 1 pottery and lithics are plotted by weight (Fig. 9), a similar overall trend is evident (in spite of some minor perturbations for lithics in Field 10). These surface findings corroborated the observations made in 1978–79, whereby the major concentration of artifacts occurred mainly in Field 8 (Fig. 4).

Data from 21 collection squares crossing Fields 8 and 9 in Corridor 2 are presented. Plots of surface pottery and lithic counts conform to one another (Fig. 10), but their distributions are distinctly different from those in Corridor 1. In Corridor 2 plots, there are two distinct peaks, one in northern Field 8 and a second in northern Field 9, while the intervening area has many fewer surface artifacts (Fig. 11). A peak in Field 8 was anticipated from the previous fieldwork; the peak in Field 9 was unexpected since that area fell outside of the boundary of the previously defined major concentration.

Excavations

In February 1979, a single 2×2 m excavation unit was dug on the eastern edge of the major concentration, in a pasture due east of the cement block building (Fig. 4). Deposits were dug in 10-cm levels within the three strata (I–III) identified. The upper 20 cm of Stratum I was a mixed deposit of historic and prehistoric artifacts. Below this disturbed level, prehistoric deposits were intact to 80 cm (Stratum III) although cultural materials were most abundant to 60 cm, in Stratum II (Watters, 1980:table 17).

In 1990, the first ten test pits (0.5×0.5 m) were excavated south of the airport road in Fields 1, 2, and 3. Test pits were aligned within transects and were widely

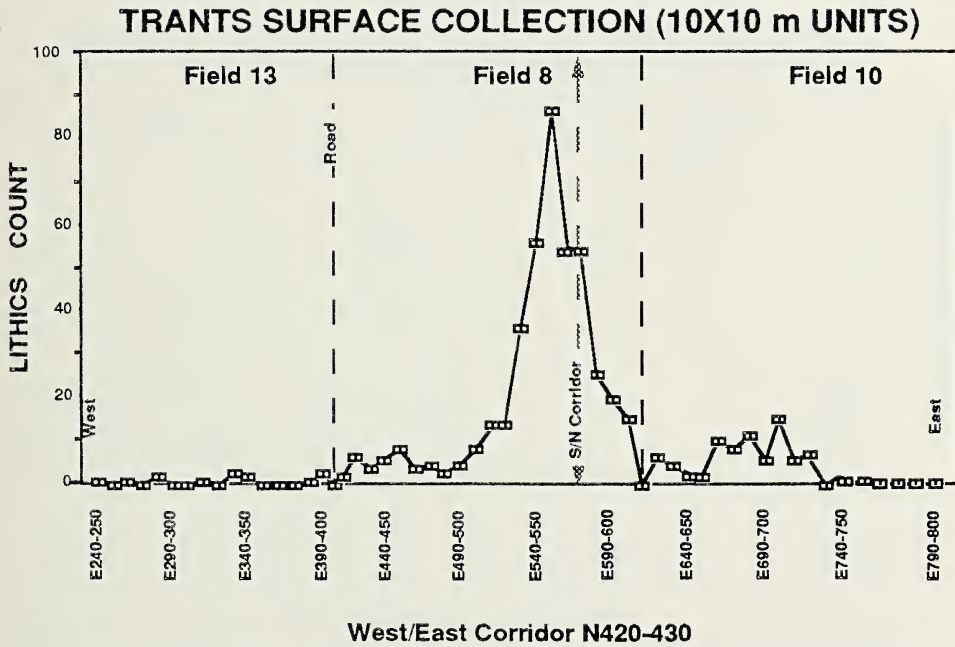
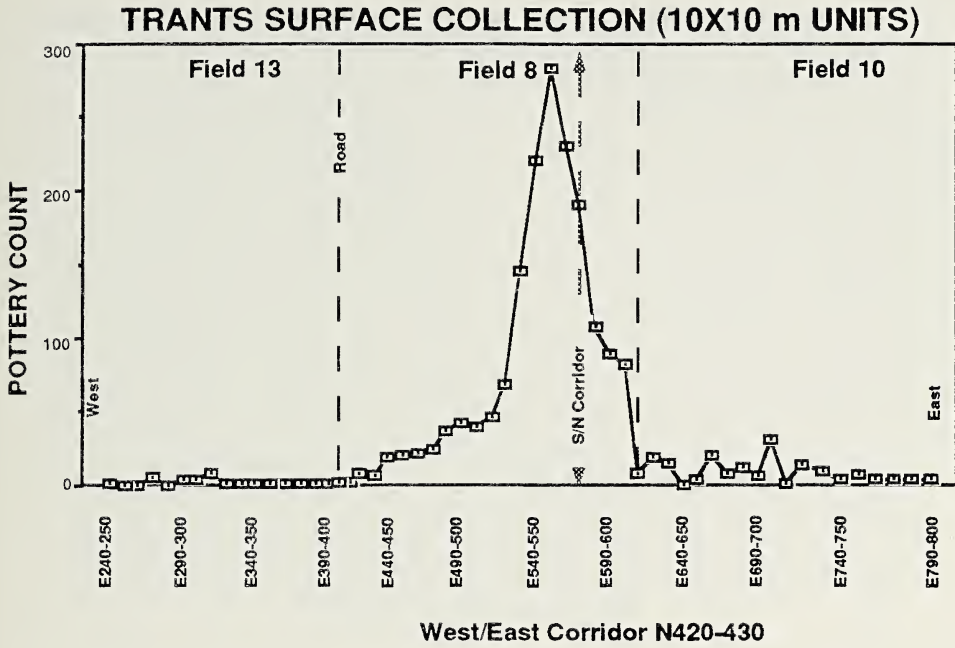


Fig. 8.—Surface pottery and lithic distributions by count in Corridor 1 (west to east) through Fields 13, 8, and 10.

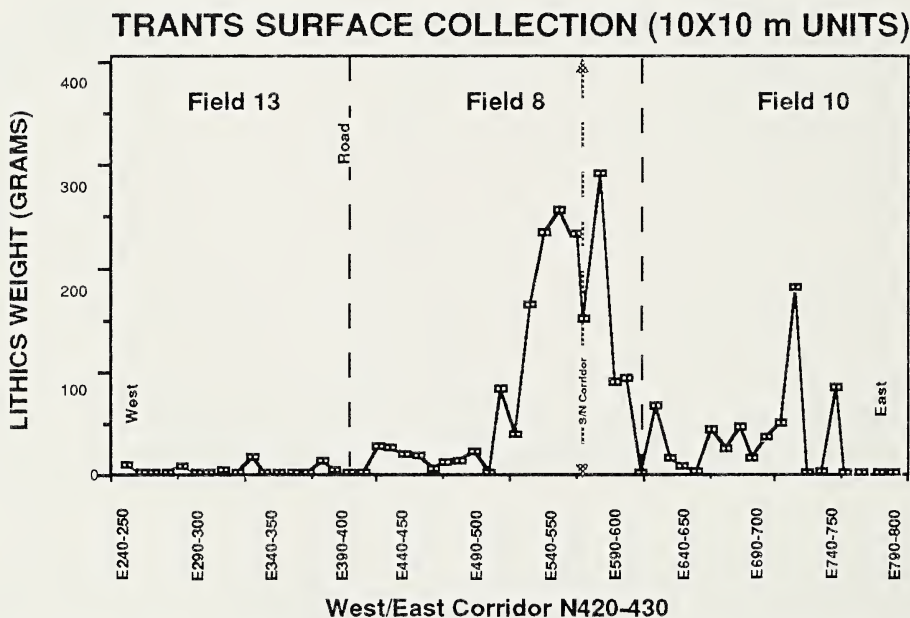
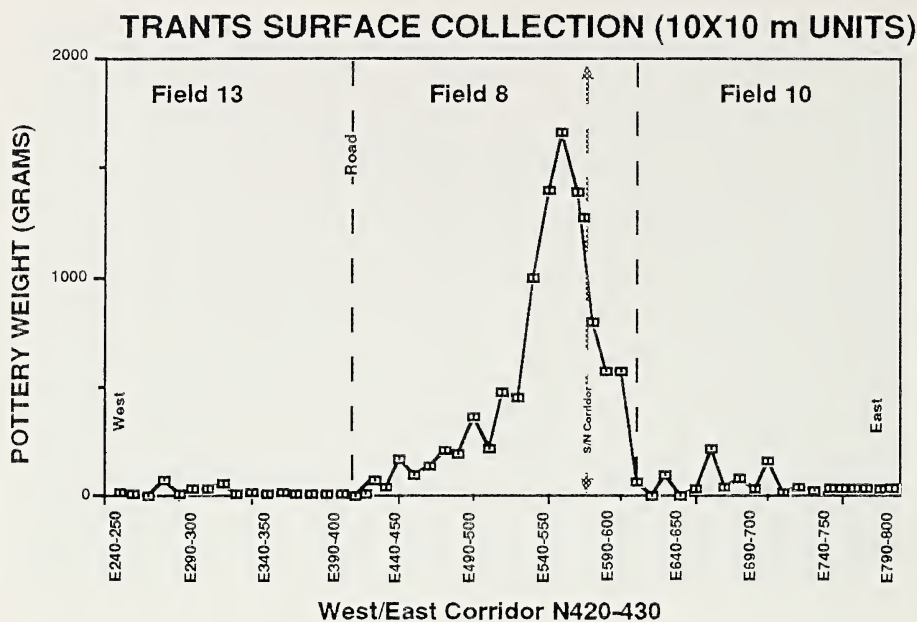


Fig. 9.—Surface pottery and lithic distributions by weight in Corridor 1. Minor lithic “peaks” in Field 10 are the result of weighty cores found on the surface of those collection units.

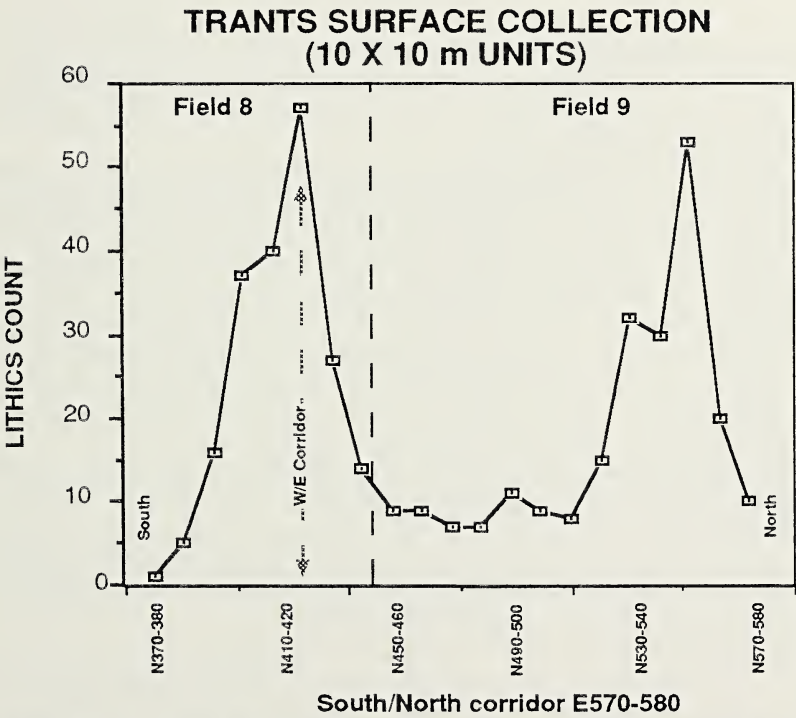
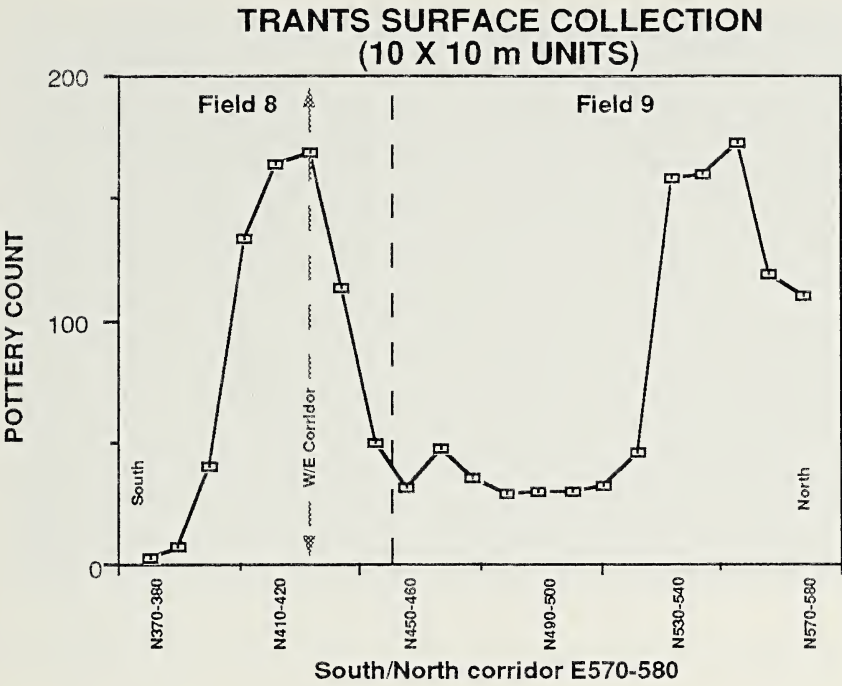


Fig. 10.—Surface pottery and lithic distributions by count in Corridor 2 (south to north through Fields 8 and 9) showing two peaks with a drop in artifact frequency in the intervening area.



Fig. 11.—Corridor 2 flags in Field 9 (looking north). Note the high density of flags (indicated by the arrow), correlating to the artifact peak in the north part of Field 9, compared to the sparsely distributed flags in that field's central and southern parts (foreground).

dispersed in the fields. The basal depths of prehistoric materials ranged from as shallow as 20 cm to as deep as 70 cm; cultural deposits extended deeper than 30 cm in only three test pits (Table 1). The quantities of artifacts within these test pits were correspondingly limited.

The collection corridors revealed differentially distributed surface artifact densities in Fields 8, 9, 10, and 13. However, one concern was that these distributions might have been biased by surficial disturbance caused by cultivation, including sugar cane grown during the historic period and sea island cotton more recently. To investigate the possibility of biased surface distributions, a systematic subsurface testing program was used in the same two collection corridors. A test pit (0.5×0.5 m) was dug every 50 m along the entire length of each corridor. This testing program made it possible to compare the subsurface distributions in test pits across the site; it also provided a means to compare surface and subsurface artifact distributions within each collection corridor.

In the five test pits dug in Corridor 2, one in Field 8 and four in Field 9, the basal depths of prehistoric artifacts ranged from 50 to 100 cm (Table 1). Pottery and lithic plots (Fig. 12) reveal a definite frequency decrease that correlates very well with the decrease seen in the Corridor 2 surface data (Fig. 10). The low density area in each data set corresponds to the southcentral part of Field 9, where the shallowest test pit also is located (Table 1).

Twelve test pits were dug in Corridor 1, four each in Fields 13, 8, and 10. Shallower test pits generally occurred in Field 13 and the eastern part of Field 10 (Table 1). These test pits also yielded lesser quantities of pottery and lithic artifacts (Fig. 13). The peak in the eastern part of Field 8, which was anticipated based on the surface collected data, was present. However, a second peak for subsurface

Table 1.—*Excavations at the Trants site in 1979 and 1990.*

Field	Location	Pre-historic depth (cm)	Remarks
1979 excavation unit (2.0 × 2.0 m)			
10	east edge of major concentration	80	prior to 1990 site grid
1990 test pits (0.5 × 0.5 m)			
a. South of airport road (<i>n</i> = 10)			
1	T1P1	70	T = Transect; P = Test Pit
1	T1P2	30	
1	T2P1	60	
2	T3P1	30	
2	T3P2	20	
2	T3P3	30	
3	T4P1	40	
3	T4P2	20	
3	T4P3	20	
3	T5P1	30	
b. Corridor 1 test pits (<i>n</i> = 12; west to east)			
13	N421 E245 SE	20	
13	N421 E295 SE	40	
13	N421 E345 SE	40	
13	N421 E395 SE	50	
8	N421 E445 SE	30	
8	N421 E495 SE	60	
8	N421 E545 SE	50	
8	N421 E595 SE	60	
10	N421 E645 SE	110	adjacent to unit N421/422 E645
10	N421 E695 SE	60	
10	N421 E745 SE	30	
10	N421 E795 SE	50	
c. Corridor 2 test pits (<i>n</i> = 5; south to north)			
8	N395 E571 NW	100	adjacent to unit N396 E571
9	N445 E571 NW	60	
9	N495 E571 NW	50	
9	N545 E571 NW	60	
9	N595 E571 NW	60	adjacent to unit N596 E571
d. Discretionary test pits (<i>n</i> = 2)			
10	N407 E634 SW	80	near 1979 excavation unit
10	N521 E646 SW	100	
1990 excavation units (1.0 × 1.0 m)			
a. Corridor 1 excavation unit			
10	N421/422 E645	110	adjacent to test pit N421 E645 SE; the unit quadrants excavated are N421 NE and NW and N422 SE and SW
b. Corridor 2 excavation units			
8	N396 E571	100	adjacent to test pit N395 E571 NW
9	N596 E571	100	adjacent to test pit N595 E571 NW

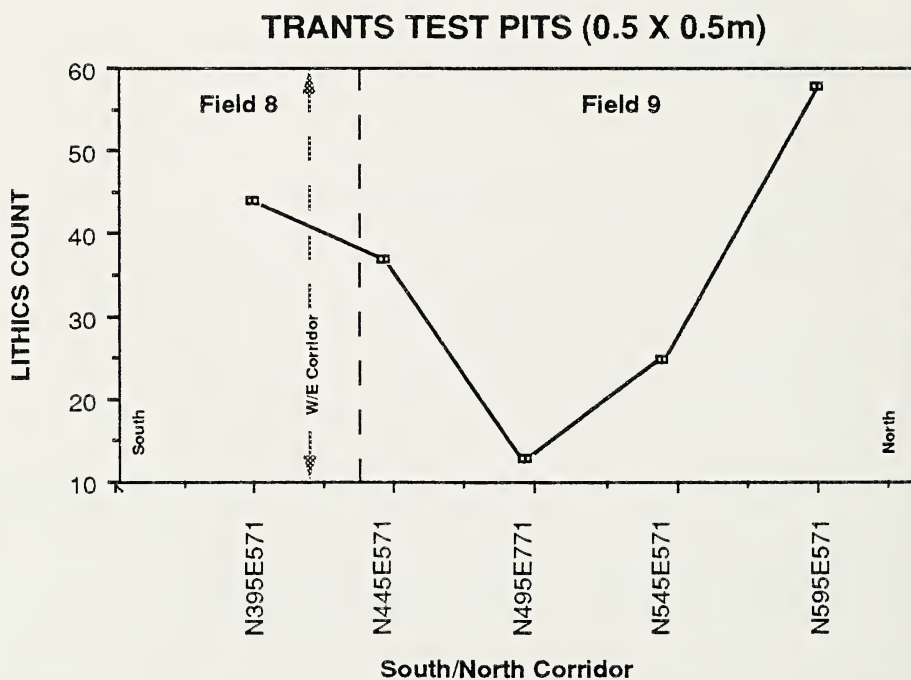
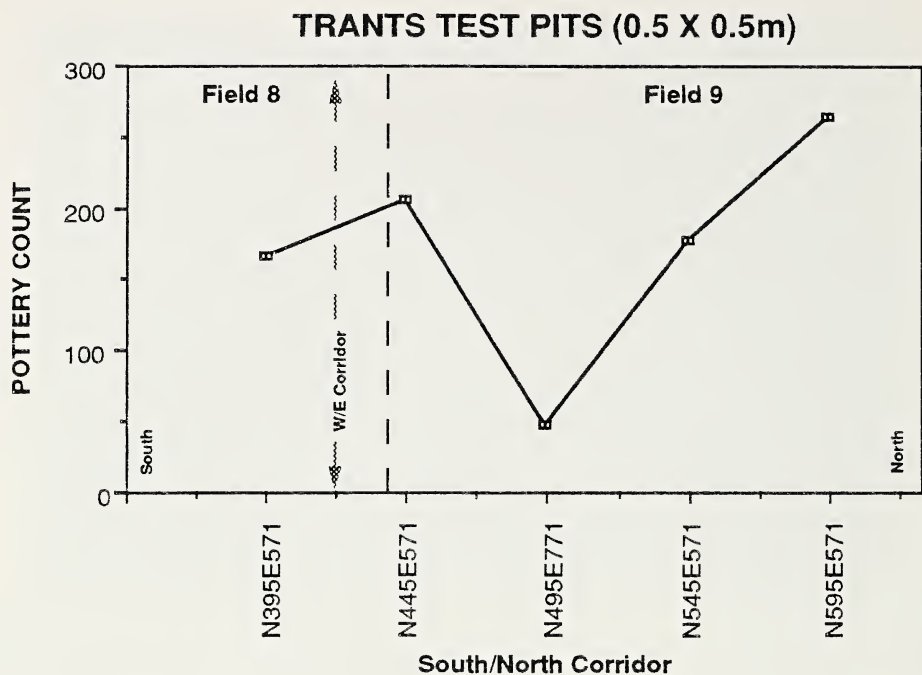


Fig. 12.—Subsurface pottery and lithic distributions by count for the five test pits in Corridor 2, once again displaying the marked decrease in artifact frequency (compare with Fig. 10).

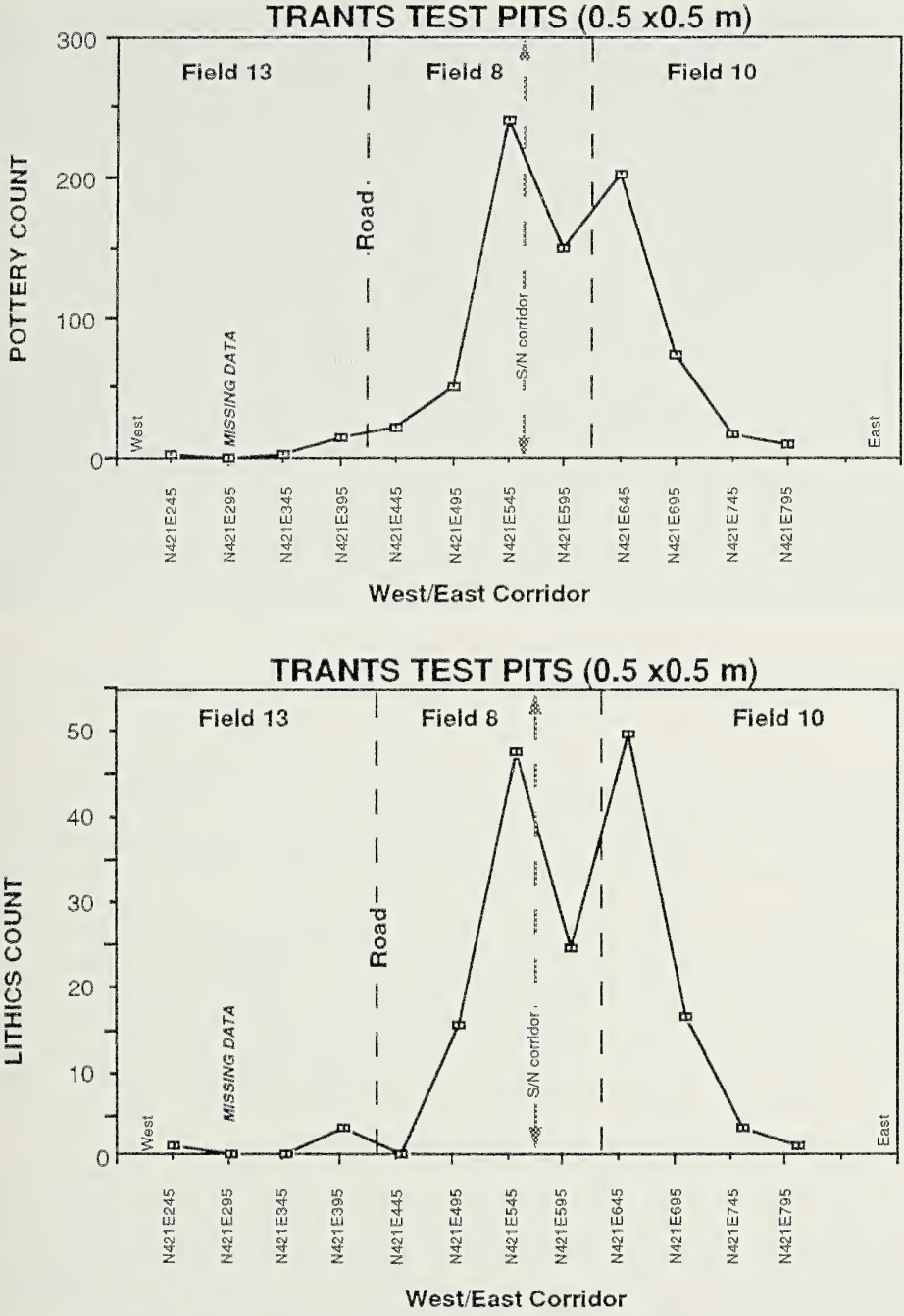


Fig. 13.—Subsurface pottery and lithic distributions by count for the 12 test pits in Corridor 1. The abundance of subsurface artifacts denoted by the peak in the west side of Field 10 is not duplicated in the surface density plots (compare with Fig. 8).



Fig. 14.—View looking west of the 1.0 × 1.0 m excavation unit (N421/422 E645) laid out beside its adjacent (already dug) test pit (N421 E645 SE) in Corridor 1 in Field 10 (see also Fig. 21).

pottery and lithics is evident in the western part of Field 10 (Fig. 13), an area where no peak was expected based on the surface data. Lithic frequency actually is slightly greater for the Field 10 peak. Equally intriguing was an unexpected frequency decrease, for both pottery and lithics, in the easternmost test pit of Field 8, between the two peaks. For Corridor 1, the overall distribution patterns for surface and subsurface artifacts across Fields 13, 8, and 10 were analogous (Fig. 8, 13). However, it was the test pit plots alone that pointed out the significance of the subsurface remains in the western edge of Field 10 for defining the extent of the site.

Two “discretionary” test pits were excavated in Field 10. One was positioned in the southern part of that field near the 2.0 × 2.0 excavation unit dug in 1979, in order to compare their stratigraphies. The maximum depth of cultural materials in this test pit was 80 cm, the same as the nearby 1979 unit (Table 1). A second discretionary test pit was dug in the northern part of Field 10, an area where no subsurface data and no systematically collected surface data were available. This test pit contained prehistoric artifacts to about 100 cm; it also yielded the only complete ceramic vessel excavated at the Trants site.

Three excavation units (each 1.0 × 1.0 m) were dug during the final phase of the 1990 fieldwork. They were dug adjacent to the three test pits providing the best stratigraphic information at key areas of the site (Fig. 14). Excavation units were placed in Field 8, northern Field 9, and southern Field 10. Prehistoric artifacts, which were recovered from three field strata (A–C) in the excavation units (Petersen and Watters, 1991), reached depths of 100 to 110 cm (Table 1). Because these excavation units are so widely dispersed, a site-wide correlation is equivocal for the three field strata identified in the three units in 1990. Also equivocal is an association between the three strata (I–III) identified in the 1979 excavation unit and the three field strata (A–C) from the 1990 units. Although stratigraphic correlations across the site cannot be made at this time, the recurrence of three strata having cultural materials in all four excavation units is noteworthy.



Fig. 15.—Panoramic view (looking SSE) of the Trants site. A, south part of airport runaway; B, cement block building in the treeline; C, Farm River, the southern border of the site; D, lower slope of the Centre Hills. Fields 1–3 and 8–13 are the primary fields mentioned in the text (compare with Fig. 5).

Mixed deposits containing historic and prehistoric artifacts were, for the most part, stratigraphically restricted to field stratum A (and Stratum I from 1979), especially to its uppermost levels (ca 0–25 cm). Beneath this mixed layer, the undisturbed prehistoric deposits yielded the kinds of artifacts and ecofacts (ceramics, lithics, bone, crab, mollusks, and coral) that routinely recur in Ceramic Age middens in the West Indies.

A total of 29 test pits, having a surface area of 7.25 m² were dug in Fields 1, 2, 3, 8, 9, 10, and 13. When the 3-m² area of the three excavations units is added, a total of 10.25 m² of surface area was excavated in 1990. Combining that total with the 4-m² surface area dug in 1979, a cumulative total of 14.25 m² of surface area has been excavated at Trants.

Field Methods Summary

In one sense, the Trants site comprises virtually all of the 60 hectares of relatively flat land stretching eastward from the mountains to the coast (Fig. 15). Surface artifacts were found in every field examined but their densities varied greatly across the site. Fields nearest to the mountains, south of the airport road, and north of the estate road had fewer artifacts. Within the broader landscape, the surface and subsurface distributions reveal a “most dense” area of artifacts, the extent of which is still not fully determined but likely encompasses major portions of Fields 8, 9, 10, and 11 (Fig. 16). This “most dense” area covers about 90,000 m² (9 hectares) and incorporates all of the “major concentration” but not the “minor concentration” defined in 1978–79. Interviews in 1990 with Montserations involved in constructing Blackburne Airport, which opened in 1957

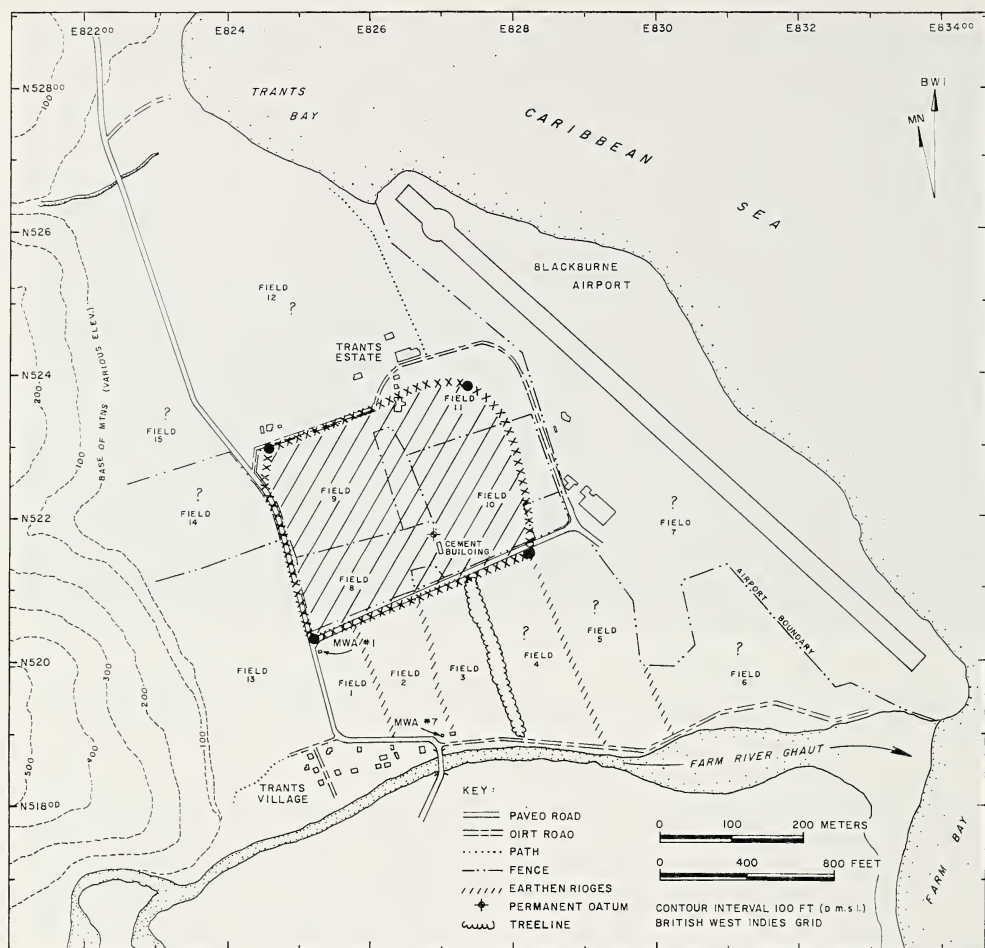


Fig. 16.—An overall “most dense” area of artifacts, within the broader terrain, covered most of Fields 8, 9, 10, and 11 (BWI grid).

(Wheeler, 1988:56), revealed that the minor concentration really was an artifact scatter exposed by bulldozers scraping the adjacent land for fill to extend the northern end of the original runway. The minor concentration, even though it is situated well away from the “most dense” area, deserves further study since the depth and extent of its cultural deposits have yet to be determined.

SITE CONFIGURATION

After the 1978–79 fieldwork, the Trants site was deemed to be a prehistoric village, the extent of which was approximately co-terminus with the major concentration (Watters, 1980:249–252). Some aspects of this view changed dramatically following the 1990 fieldwork.

The surface collection squares and test pits in Corridor 1 confirmed dense artifact distributions in Fields 8 and 10. In Corridor 2, the collection squares revealed a pattern previously unrecognized, with a significant decrease in artifact

density in the middle of the corridor and a marked increase in northern Field 9. Five test pits and two excavation units in Corridor 2 corroborated the variable densities initially observed on the surface.

The pattern that was beginning to emerge altered previous perceptions of the Trants site because, for the first time, a "core area" was recognized (Fig. 17). The highest artifact densities were obtained in two sectors, the northern sector (northern part of Field 9) and the southern sector (Field 8 and the southern part of Field 10), and these sectors are separated by 100 m of sparsely distributed artifacts (central-southern part of Field 9). The southern sector maximally extends east-west about 250 m based on Corridor 1 data. The northern sector's length is less well-determined because this part of the site had no corresponding east-west corridor, and therefore no equivalent systematically collected, quantifiable data. It has a length of at least 150 m, based on observed surface artifacts, and likely extends further eastward judging from the discretionary test pit in northern Field 10 (Fig. 17). The core area's northern and southern sectors consist of opposing but seemingly complementary curvilinear segments demarcated by dense artifact distributions.

Although the northern and southern sectors were fairly well-defined during the 1990 fieldwork, little was known about the eastern and western margins, the areas that potentially linked the two sectors. Surface artifact scatters indicated that these connections likely existed. The presence of the connecting link on the eastern margin was strongly supported by data from the discretionary test pit in northern Field 10 (Fig. 17). This isolated test pit, the sole source of information for that part of the site, attained a depth of 100 cm with clearly defined stratigraphic layers and it yielded abundant artifacts.

The western margin, in the more westerly part of Field 9, was the least known area of the Trants site at the close of the 1990 fieldwork. Corridor 2 was situated in the eastern part of Field 9 (Fig. 5) and did not traverse this western margin. In 1992, eight backhoe "trial" or "borrow" pits, dug in connection with the planned airport development, provided subsurface data about the western margin. During their brief visit to Montserrat in May 1992, Watters and Petersen were able to examine the open trial pits, which the contractor had left unfilled as requested. Four pits each had been dug in Fields 8 and 9. Two Field 9 pits (B6 and B7 on Fig. 17), located midway between the northern and southern sectors, were especially important with respect to the western margin. These pits (Fig. 18) contained midden material, including abundant artifacts and faunal remains, in stratified cultural levels that paralleled what had been observed in other excavated areas of Trants. Even more strongly than was the case for the one discretionary test pit on the eastern margin, the two borrow pits in Field 9 support the existence of the western link between the northern and southern sectors. Another trial pit, on the eastern edge of Field 9, also proved to be significant since it was located in the area of low artifact density identified in the Corridor 2 research. This pit had few cultural remains, an observation that matched the findings for the nearby shallow test pit excavated in Corridor 2 (Fig. 17).

CHRONOLOGY AND OCCUPATION

Eight radiocarbon dates, all obtained from charcoal samples in excavated contexts, are available for the Trants site. Two are from the 1979 excavation unit and six from the 1990 fieldwork (Table 2). Samples from Trants provide two of the oldest dates from the Ceramic Age in the Lesser Antilles, at 2430 ± 80 B.P.

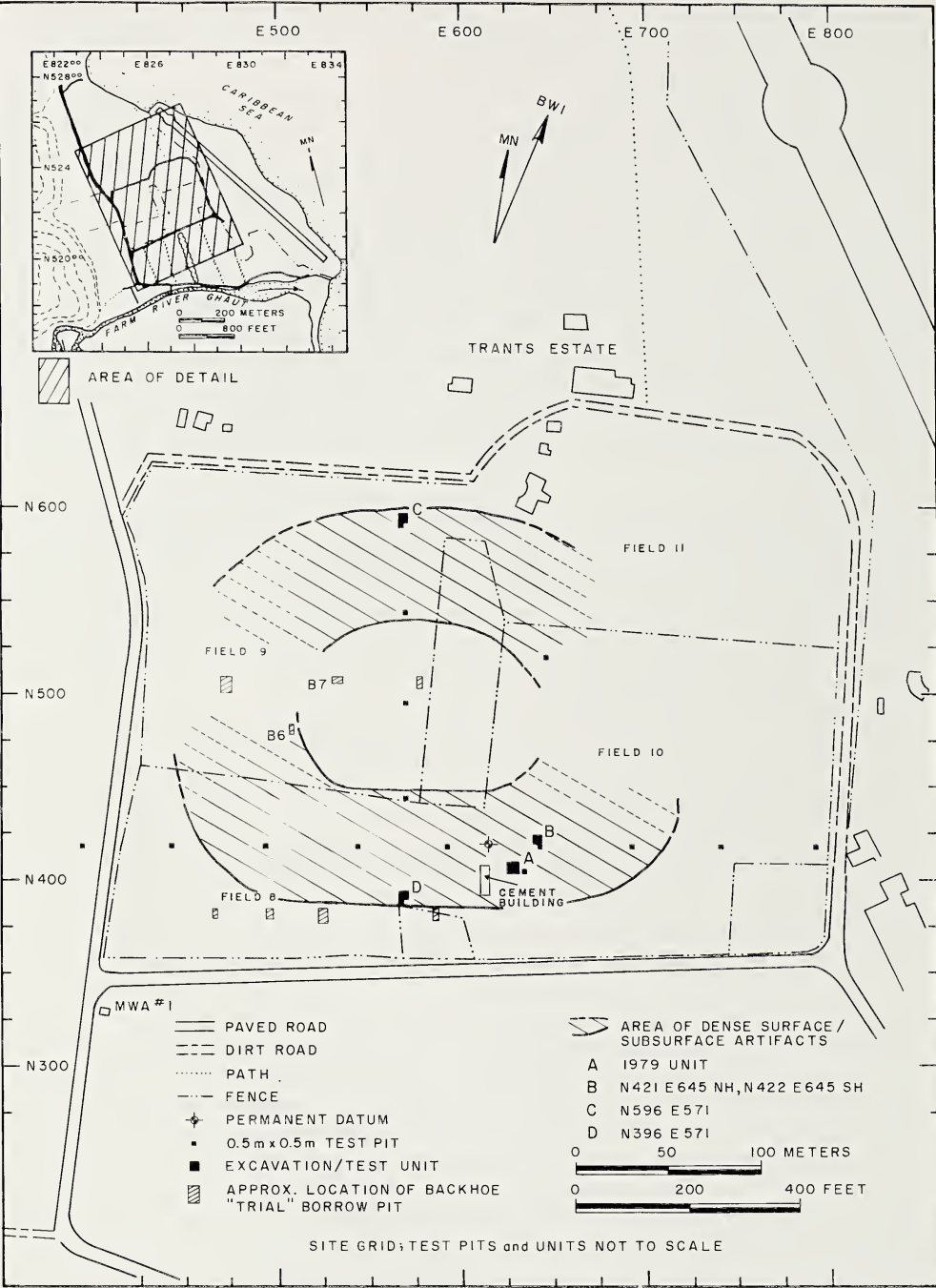


Fig. 17.—The oval-shaped “core area” of the Trants site, as demarcated by the northern and southern sectors and the less well-defined eastern and western margins (site grid).



Fig. 18.—Backhoe “trial” pit B7 dug in connection with future development of the new airport.

(Beta-44828) and 2390 ± 90 B.P. (Beta-41682), or respectively ca 480 and 440 B.C. (uncorrected), both of which were obtained from field stratum C, the deepest cultural stratum in their respective excavation units. The oldest date is from the excavation unit (N396E571) in Field 8 (Fig. 17, Unit D) of the southern sector of the site; the next oldest date is from the unit (N596E571) in Field 9 (Fig. 17, Unit C) of the northern sector; the samples are separated by 200 m. These two dates are from midden deposits in excavation units located on their respective outer edges of the opposing curvilinear sectors and midway on the circumference of the oval (Fig. 17). Another radiocarbon date for the northern sector excavation unit (Fig. 17, Unit C), 1890 ± 70 B.P. (Beta-41678), or ca A.D. 60, is from field stratum B and in correct stratigraphic relationship (Table 2).

Five radiocarbon samples from the southeast portion of the Trants site in Field

Table 2.—*Chronological ordering of radiocarbon dated samples from various contexts at Trants.*

Radiocarbon years B.P.	Conversion (uncorrected)	Lab sample	Contexts			
			Unit	Depth ^a	Field	Corridor
2430 ± 80	480 B.C.	Beta-44828	N396E571	50–70	8	2
2390 ± 90	440 B.C.	Beta-41682	N596E571	70–80	9	2
2140 ± 80	190 B.C.	Beta-18489	1979 unit ^b	40–50 ^c	10	n/a
1960 ± 90	10 B.C.	Beta-41680	N422E645	70–80	10	1
1890 ± 70	A.D. 60	Beta-41678	N596E571	30–40	9	2
1750 ± 80	A.D. 200	Beta-41679	N407E634 ^d	40–60	10	n/a
1740 ± 90	A.D. 210	Beta-41681	N422E645	61	10	1
1620 ± 90	A.D. 330	Beta-18582	1979 unit ^b	40–50 ^c	10	n/a

^a Depth in cm below ground surface.

^b This unit was dug in 1979, prior to laying out the site grid.

^c Same stratigraphic level for these two dates.

^d This discretionary test pit was not within a corridor.

10 are dated. Two dates are from the same level (40–50 cm in Stratum II) in the 1979 excavation unit (Fig. 17, Unit A), 2140 ± 80 B.P. (Beta-18489) and 1620 ± 90 (Beta-18582), or respectively ca 190 B.C. and A.D. 330 (Table 2). These widely divergent dates, separated by 520 rcy, may result from the small sample sizes. To try to resolve the problem of the discordant dates, a charcoal sample was submitted from field stratum B (40–60 cm) of the discretionary test pit in southern Field 10, the test pit nearest the 1979 unit. This procedure assumes stratigraphic correlation between Stratum II from 1979 and field stratum B from 1990. The derived date, 1750 ± 80 B.P. (Beta-41679) or ca A.D. 200, accords more closely with the younger date (A.D. 330) of the 1979 unit. The final two dates, 1960 ± 90 B.P. (Beta-41680) and 1740 ± 90 B.P. (Beta-41681), ca 10 B.C. and A.D. 210, are from field stratum C in the single Corridor 2 excavation unit (N422E645) in Field 10 (Fig. 17, Unit B). These two dates are in proper stratigraphic context.

Temporal and spatial aspects of the radiocarbon dates merit discussion. Samples separated stratigraphically have the correct temporal relationship in two excavation units. Two samples from one level in another excavation unit produced discordant dates, and it is the older (190 B.C.) of the two dates that is suspect, based on crossdating of a stratum in a nearby test pit. These eight dates (Table 2) span either 810 rcy or 690 rcy depending on the terminal date used (A.D. 330 or A.D. 210, respectively). If the suspect 190 B.C. date in the 1979 unit is ignored, the four remaining dates from the southeast part of the oval (Field 10) span 340 rcy (10 B.C.–A.D. 330). Three of those four dates fall within a 130 rcy span (A.D. 200–330). The units producing the Trants site's two oldest dates are located further west, midway across the northern and southern sectors of the oval in Fields 8 and 9 (Fig. 17). The northern unit also has one date (A.D. 60) contemporary with the earlier part of the 340 rcy span from Field 10. There are no dates from the western part of the Trants site.

Ceramics recovered during the 1978–79 and 1990 field seasons include white-on-red (WOR) painted and zoned-incised-crosshatched (ZIC) sherds (Fig. 19, 20). Such decoration is regarded as diagnostic of the Saladoid ceramic series, and as evidence for the earliest Ceramic Age population movement into the Caribbean (Rouse, 1992; Siegel, 1991). Although the decorated sherds are useful diagnostically, they constitute only 7.5% of the 1990 ceramic sample from Trants studied so far; even when slipped sherds (that otherwise are undecorated) are added to

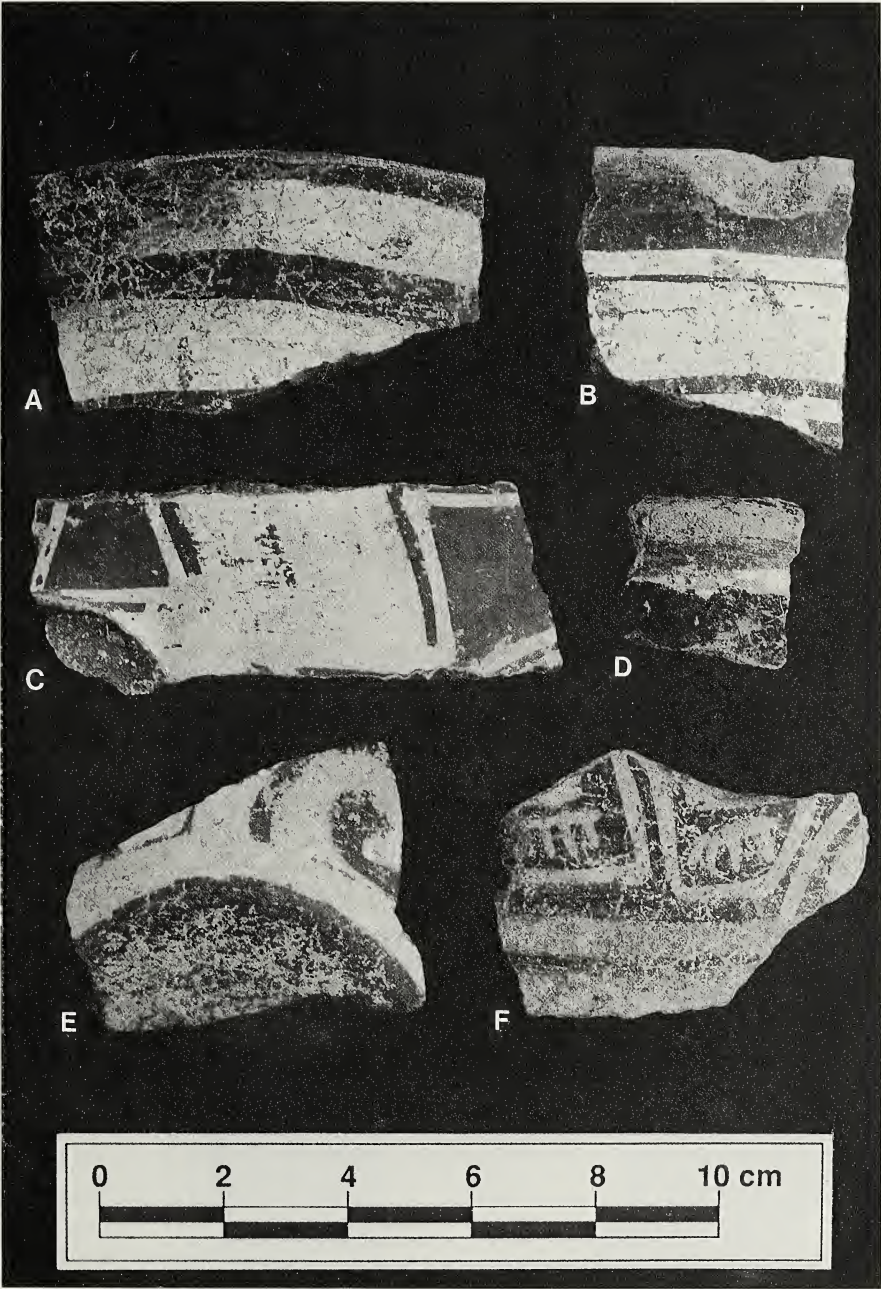


Fig. 19.—Six white-on-red painted sherds recovered from the 1979 excavation unit. Artifact FSNs (Field Specimen Numbers): A, MS-G1-955; B, MS-G1-510; C, MS-G1-953; D, MS-G1-788; E, MS-G1-572; F, MS-G1-966. (Photograph courtesy of James B. Petersen.)

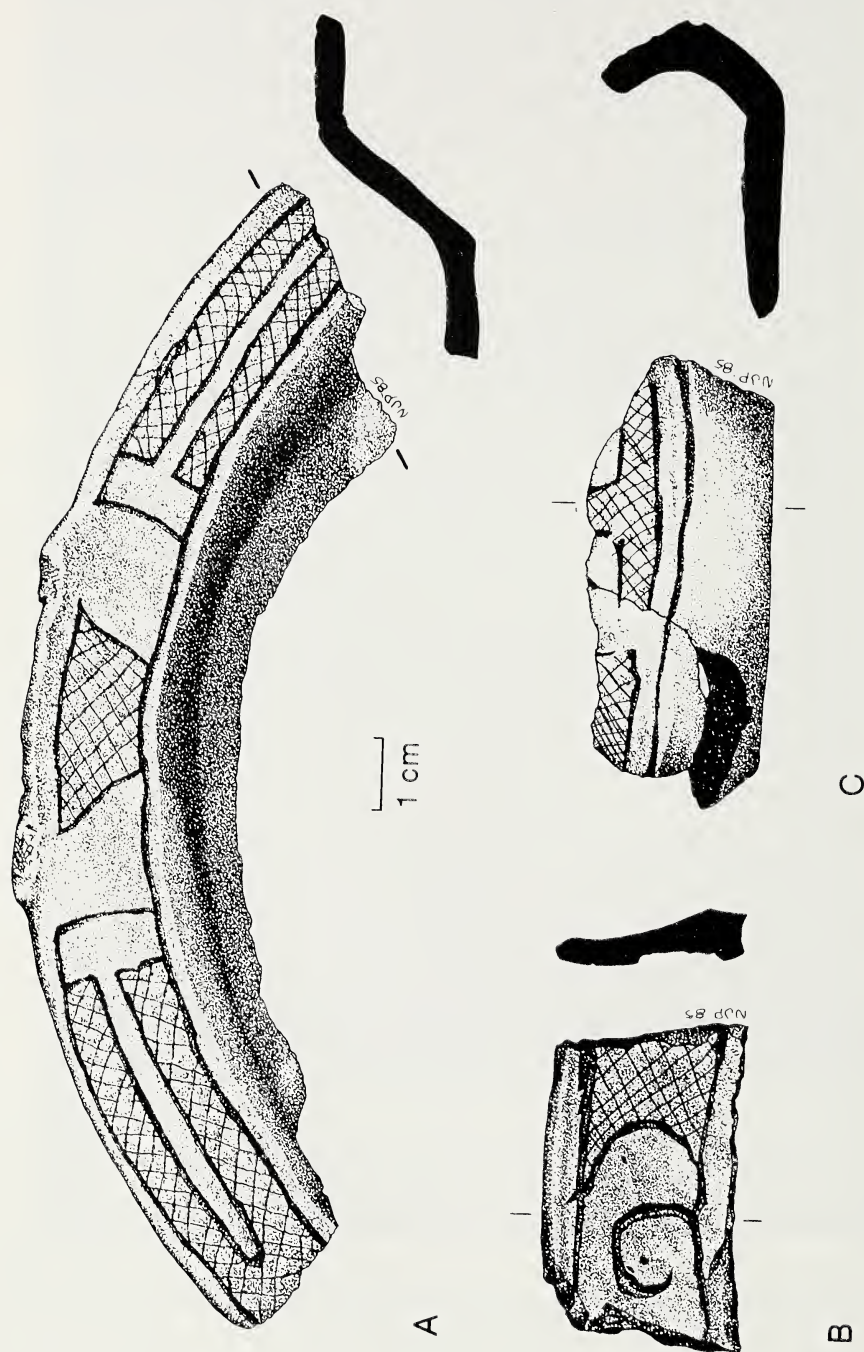


Fig. 20.—Three renderings of zoned-incised-crosshatched sherds recovered from the 1979 excavation unit. Artifact FSNs: A, MS-G1-806; B, MS-G1-476; C, MS-G1-292 and MS-G1-293.

decorated sherds, the cumulative total is only 14.4% (Petersen and Watters, in press). At Trants, WOR and ZIC sherds commingle in excavation units and test pits rather than being spatially segregated.

The radiocarbon dates and diagnostic artifacts confirm an early Ceramic Age occupation at Trants, generally corresponding (but beginning earlier) to Period IIa (300 B.C.–A.D.400) in the chronological framework established by Rouse (1992:fig. 26). The field research carried out to date cannot answer, with certainty, whether the Trants site was inhabited continuously or occupied intermittently during the 810 (or 690) rcy span. Also uncertain is whether the oval was formed simultaneously, resulting from a single habitation event that was spatially contiguous, or was formed episodically, resulting from multiple habitation events that were spatially discontinuous but which eventually coalesced to create the oval. The configuration of the oval (assuming full closure on the eastern and western margins) is certain; the site formation processes that created the oval are uncertain. Early Ceramic Age occupation at Trants is certain; the continuity of that occupation is not.

DISCUSSION

Field Methods

The collection corridor technique was the most efficient (in terms of time expended) and effective (in terms of quantifiable data secured) of the systematic surface collection strategies used at the Trants site. It provided the broadest coverage of the terrain and distinguished the “most dense” and “core area” from that terrain. The 10 × 10 m collection squares were laid out rapidly using tapes and chaining pins; artifacts in each square were quickly pin flagged, counted, and collected; and photographs taken of the individual squares and the corridors provided permanent visual records of the relative densities of flagged artifacts (Fig. 7, 11). The corridor technique did result in the forfeiture of certain provenience data, notably the loss of precise locations for the surface artifacts within each square. Loss of these data was deemed acceptable since the site surface already had been disturbed by cultivation, thereby making that level of precision somewhat inconsequential and superfluous.

The collection corridor technique proved to be effective but it could have been even more efficient. Surface artifact density plots (Fig. 8, 9) for Corridor 1 show that two patterns, one of artifact scarcity in Fields 13 and 10 and one of abundance in the east part of Field 8, would have been detectable even when the total number of collected squares was reduced considerably. In the CMNH-UMF project, every square ($n = 56$) was collected for the entire length of Corridor 1. Yet, the overall distribution would still have been evident even if only every second square ($n = 28$) or perhaps every third square ($n = 18$) had been collected instead. The same rationale applies to the 21 collection squares in Corridor 2 (Fig. 10). Had the conformity of the patterns been recognized during the fieldwork at the Trants site in 1990, the “skipping” squares rationale could have been used in Corridors 1 and 2, thereby freeing up time for doing additional east–west and north–south collection corridors and thus providing even more extensive spatial coverage of the terrain and site.

Although the same rationale theoretically could be applied to corridor test pits, an examination of the plots indicates a decision to skip certain test pits would result in different distribution patterns. Skipping any test pit would have been a precarious exercise in Corridor 2 since it contained only five test pits (Fig. 12).

Increasing the interval between the 12 test pits in Corridor 1 would modify its overall pattern less drastically than Corridor 2, and skipping one or two test pits in Field 13 would not have greatly affected the low-density pattern observable in that particular field (Fig. 13). However, had the single test pit in westernmost Field 10 been skipped over, its elimination would have obscured completely the "unanticipated" subsurface peak which originally called attention to the eastward extension of the site. For the "most dense" and "core area" at Trants, a 50-m space between test pits appears to be the minimum interval needed to maintain the integrity of the subsurface density pattern. The low-density peripheral fields are suitable for more widely spaced test pits.

The collection corridor strategy corroborated some previous findings such as the major concentration existing in Field 8, but it also revealed new information on artifact distributions, such as the frequency decreases in surface and subsurface artifacts in Corridor 2 and the eastward extension of the site into Field 10. This technique certainly fulfilled the objectives of demarcating the extent and defining the boundaries of the Trants site, but it could have been made even more efficient, by reducing the number of surface collected squares, without compromising the integrity of the overall surface distribution patterns in each corridor.

Spatial Parameters

At the close of the 1990 CMNH-UMF project, the investigated terrain was interpreted as three spatially distinct areas. The first, the *peripheral area*, was demarcated by the modern fields having sparsely distributed surface artifacts. The low-density determinations resulted either from systematic sampling or from less reliable superficial observations made while walking over certain fields. The peripheral area encompassed Fields 1–6 south of the airport road, Field 12 north of the estate road, and Fields 13–15 at the base of the mountains (Fig. 5). Field 7, the Blackburne Airport, was the only part not observed at all in the entire 60-hectare terrain.

The second distinctive area, the *most dense area*, comprises the higher-density distributions determined primarily from the surface artifact plots in Corridors 1 and 2. The most dense area incorporates almost all of Fields 8, 9, 10, and 11 (Fig. 16). Its maximum extent likely is somewhat biased along the northern, western, and southern boundaries by artifacts that were brought to the surface through construction of the roads that correspond to those borders.

The third distinctive area is the *core area* which lies wholly within the most dense area. It certainly incorporates parts of Fields 8, 9, and 10 and probably part of Field 11 (Fig. 17). The circumference of the core area includes the fairly well-defined, curvilinear-shaped northern and southern sectors and the suggestive, but less firmly established, linking sectors on its eastern and western margins. The one discretionary test pit in northern Field 10 and the two trial pits in Field 9 substantiate the existence of these connections. The boundaries of the core area delineate an oval configuration having an east–west length of as much as 250 m and north–south extent of 200 m. The middle of the oval is the low-density area identified in the Corridor 2 plots. The size of the core area alone (50,000 m², or 5 hectares) is larger than the total site area (42,500 m²) estimated after the 1978–79 fieldwork.

In overview, the peripheral area comprises the relatively flat 600,000-m² terrain, bounded by the mountains, coast, and river valley, in the midst of which is the

most dense area of 90,000 m² which in turn encompasses the 50,000-m² core area of the Trants site itself.

Oval Configured Sites

Analysis of spatial patterning in this article relies primarily on artifact distributions and secondarily on radiocarbon date distributions. Another data set, sediment analyses and distributions, provides independent support for the existence of the peripheral area, in which low artifact densities and low sediment values correlate, and the core area, in which high artifact densities, high sediment values, and the occurrence of anthrosols also correlate. Petersen and Watters (1991) presented the sediment data in a preliminary manner; a detailed analysis of grain size characterization, pH, organic matter, and phosphate fractionation will be provided by Petersen in a separate part of the Trants field research series.

Within the core area of the Trants site are two well-defined areas, the northern and southern sectors (apparently extending to the eastern and western margins) consisting of middens with high densities of artifacts and ecofacts and high sediment values, and a site center comprising a 100-m-diameter area with low artifact density. Although the site center is thought to represent an area of "common ground" or "community space," it is premature to label this area a "plaza" or "dance-court" (cf. Alegría, 1983).

The Trants site's oval configuration is demarcated by the encircling middens. The two oldest dates (480 and 440 B.C.), from excavation units opposite one another on the oval, indicate contemporaneous occupation for those particular points along the northern and southern sectors. Four other dates indicate more recent habitation of the oval's southeast segment. Presently undated are other midden segments on the oval's circumference and the site center.

Circular, ring, or oval configured sites occur elsewhere in the Caribbean. Siegel (1992:372) uses a concentric "ring model" to characterize the Maisabel site on the north coast of Puerto Rico (Fig. 2). The site plan (Siegel, 1992:fig. 6.2) depicts a "cleared central portion of the village," encircled by a "dense midden accumulation" (incorporating five mounded middens), in turn surrounded by a "low dense midden accumulation defining site periphery." Low densities of artifacts in the central portion and the periphery contrast with the high density midden accumulation. A cemetery was discovered in the central portion of the Maisabel site. Siegel (1992:126–132, 188–191) contends that: (1) the overall settlement groundplan was established during initial occupation by Saladoid colonists; (2) the four areas of the site he studied were occupied contemporaneously; and (3) the site was continuously occupied. Saladoid and Ostionoid occupation (ca 100 B.C.–A.D. 1200) at Maisabel spans part of Period IIa and all of Periods IIb, IIIa, and IIIb in Rouse's (1992) scheme. The Puerto Rican site of Punta Candelero, which has an earlier Huecan component with linearly arranged mounds, attains a semicircular configuration during its later Cuevas component (Rodríguez, 1991: fig. 6).

The Golden Rock site on St. Eustatius (Fig. 2) apparently had a circular layout (Versteeg and Schinkel, 1992:212). The report summarizes the spatial data derived from research by De Josselin De Jong in 1923, during which he mapped five distinct midden clusters. Three clusters subsequently were damaged by airport development. One extant cluster (GR-1), the focus of excavations in the 1980s, contained a midden, house structures, and burials; a presumably complementary

midden cluster (GR-2) is situated opposite GR-1 (Versteeg and Schinkel, 1992: fig. 178). Occupation (ca A.D. 600–800) at Golden Rock is primarily Period IIIa but may extend back into Period IIb.

Rouse (1974:167, 1978:703) characterizes the Indian Creek site on Antigua (Fig. 2) as an oval ring or a circle, with a concentration of shell refuse in a series of five middens around the periphery of an oval area. Radiocarbon dates indicate that Indian Creek encompasses the latter part of Period IIa and all of Periods IIb, IIIa, and IIIb. Rouse (1974:168) mentions two other oval-shaped sites surrounded by middens, Ostiones on Puerto Rico and Carrier in Haiti.

The oval configured core area at the Trants site most closely parallels the “ring model” at Maisabel (Siegel, 1992:fig. 6.2), with respect to their comparable low-density site centers, high-density midden areas, and low-density peripheries. Spatially distinct mounded middens at Maisabel, midden clusters at Golden Rock, and middens at Indian Creek and Punta Candelero have no counterparts yet identified at Trants, where the midden accumulation is continuous around the oval rather than existing as discrete entities. Structural remains have yet to be detected at Trants but the area where they most likely would occur, at the interface of the site center and midden areas based on findings at Maisabel and Golden Rock, has received minimal subsurface testing. A counterpart at Trants for the Maisabel cemetery within the site center is also unknown. Although comparisons between specific intrasite components at Trants and Maisabel are not warranted at this time, their strikingly similar overall configurations suggest future comparisons, following larger-scale excavations at Trants, will be fruitful.

Montserrat's Ceramic Age Sites

Trants is one of the oldest Ceramic Age sites in the Lesser Antilles. Only two sites, Hope Estate on St. Martin (560 B.C.) and Fond Brûlé on Martinique (530 B.C.), report older Ceramic Age radiocarbon dates. The dates from Trants and from these islands support a migration by ceramic-producing peoples into the Lesser Antilles at a much earlier date (by at least 500 years) than was previously accepted (Rouse, 1989; Siegel, 1991). Trants is an important component of this 500 B.C. population movement.

Equally important for establishing this population movement are the other early Ceramic Age sites on Montserrat. The Radio Antilles site (MS-A1) on the island's south coast (Fig. 2) has a single radiocarbon date, 2390 ± 60 B.P. (Beta-18491), or 440 B.C. (uncorrected), equivalent to the second oldest date from Trants. There are two other early dates from Radio Antilles, 2210 ± 70 B.P. (Beta-18490) and 2120 ± 60 B.P. (Beta-10582), or respectively 260 B.C. and 170 B.C. Excavations at Trants and Radio Antilles have produced numerous examples of commingled WOR and ZIC sherds as well as vessel forms associated with the Saladoid ceramic series.

More recently, a third Montserrat site containing Saladoid ceramics, the Belham Valley site on the island's west coast (Fig. 2), has been identified from artifacts surface collected in 1964 by Walter Kenyon and curated at the Royal Ontario Museum (ROM). During Kenyon's visit, the Belham Valley site was in the process of being covered over (perhaps destroyed) by grading for a golf course. In 1979, informants notified Watters (1980:237) of the existence of the Belham Valley site but his reconnaissance of the golf course fairways failed to detect any surface artifacts. The materials in the ROM collection are the only artifacts from this site available for study. The Belham Valley collection, kindly loaned by ROM to



Fig. 21.—Stratigraphy of the east wall (1.5 m length) of the excavation unit and its adjacent test pit in Field 10 (see also Fig. 14).

CMNH for the past two years, has been studied by Petersen and Watters. It includes 300 individual vessels, defined primarily by rim sherds, and contains painted, incised, and undecorated sherds ascribed to the Saladoid ceramic series. Diagnostic WOR and ZIC artifacts confirm that Belham Valley is Montserrat's third early Ceramic Age site. The absence of materials suitable for radiocarbon dating in the ROM collection means that more precise information on the duration of occupation at Belham Valley is unavailable.

Early Ceramic Age colonization of Montserrat is documented by Saladoid ceramics in three very widely dispersed sites on relatively flat land occurring near sea level on the east, south, and west coasts (Fig. 2). Radiocarbon dates at the sizeable sites of Trants and Radio Antilles document early settlement and suggest these occupations were sustained. The area and duration of occupation of the Belham Valley site are unknown, but the site's location in the largest valley on the island and its proximity to the largest permanent flowing river suggest it also was a major habitation site. The other prehistoric sites on Montserrat, Windward Bluff, Farnsworth, Dagenham Beach, and Little Bay, are more recent post-Saladoid sites containing no Saladoid ceramics.

CONCLUSIONS

The Trants site presently is interpreted as a manifestation of the initial Ceramic Age population movement into the Lesser Antilles at about 500 B.C. Small scale excavations (Fig. 21) within the core area recovered common midden materials such as pottery, lithic tools and debitage, shell and stone beads, and a variety of vertebrate, molluscan, crab, and coral remains. The pottery is attributed primarily

to the early part of the Saladoid ceramic series (Petersen and Watters, in press). Late Saladoid and post-Saladoid ceramics are absent in the Trants excavations.

Spatial distribution of the two oldest radiocarbon dates, one each from the northern and southern midden sectors, indicates occupation was contemporary in these areas of the Trants site. The site's terminal date (A.D. 330) provides a timespan of some 810 rcy, which incorporates almost all of Period IIA and extends back into latest Period Ib. Dates ranging from 10 B.C.–A.D. 330 on the oval's southeast part support the idea of a sustained occupation in that sector. Whether the site was inhabited continuously or occupied intermittently during that 810 rcy span is uncertain.

Surface and subsurface artifact distributions and sediment distributions delineate a "core area" having an oval-shaped configuration (assuming full closure on the eastern and western margins) with maximum dimensions of about 250 × 200 m. The intervening area (ca 100 m between the northern and southern sectors) exhibits definite decreases in surface and subsurface artifact densities as well as lower sediment values. Whether the oval configuration was laid down simultaneously or episodically at Trants is uncertain. Younger oval- or circular-shaped sites are reported from Golden Rock, Indian Creek, Maisabel, and Punta Candelero. These sites for the most part are more recent than the earliest dates at Trants although the Indian Creek, Maisabel, and Punta Candelero (Huecan component) sites include occupations in the later part of Period IIA.

The postulated overall site structure at Trants includes a centrally located "common ground" (the site center having sparse artifacts) that is surrounded by structures (yet to be detected) behind which are refuse areas (represented by the middens), all being contained in the core area of the site. Beyond the midden accumulation is the site periphery, which is indicated by the modern fields having low-density artifact distributions.

Field methods used in the 1990 CMNH-UMF project, notably the collection corridor strategy for surface and subsurface sampling, fulfilled the objectives of delineating the extent of the Trants site and determining its overall configuration and boundaries. This field research has verified that Trants is one of the oldest early Ceramic Age sites in the Lesser Antilles, and forthcoming parts of the Trants series will show that Trants also is one of the best-preserved sites in the region.

ACKNOWLEDGMENTS

Research in 1978–79 was supported by a Fulbright-Hays Doctoral Dissertation Research Abroad Fellowship (DHEW:OE) and an Andrew Mellon Pre-doctoral Fellowship from the University of Pittsburgh. The 1990 research was funded by the Netting and O'Neil Research Funds of Carnegie Museum of Natural History (CMNH), the Center for Latin American Studies (University of Pittsburgh), and the University of Maine at Farmington (UMF). The project was co-directed by James B. Petersen; the field crew included Cathy Watters, Robert Bartone, Elizabeth Subin, John Crock, and Ellie Cowie, and, for frequent on-site consultations, Jah Rebel. James B. Richardson III assisted with the 1992 trial pit study. The author acknowledges the Government of Montserrat for authorizing the fieldwork, and Ken Sparkes, then Director of Public Works, for providing plans of the proposed airport development; the Montserrat National Trust, especially its President Franklin Margetson, for serving as liaison with Government and issuing the export permit for artifacts analyzed in the U.S.; Erica Gibbs for providing the crew with delightful field accommodations; Cedric and Carol Osborne, Bert and Marion Wheeler, and Parker and Meg McChesney, for assistance and advice on various matters; Mrs. Sarita Weekes-Francis and Grace White for arranging site visits by students from Salem, Harris, and Bethel schools; Elizabeth Subin, Robert Bartone, and John Crock (UMF) and Tara Reilly, Andrew Fisher, and Ann Fleming (CMNH) for laboratory assistance; Belinda Cox (UMF), Carrie Pantier, Nancy Perkins, and Gail Richards (CMNH) for graphics; and Sylvia Keller (CMNH) for preparation of tables. The author acknowledges the careful reading and constructive criticism of the reviewers.

Earlier versions of this paper were presented in 1993 at a Trants symposium at the Society for American Archaeology annual meeting in St. Louis and at the 15th International Congress for Caribbean Archaeology, San Juan, Puerto Rico.

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ARCHAEOLOGY OF TRANTS, MONTSERRAT. PART 2.
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ABSTRACT

Trants (MS-G1) is a Saladoid site located on the island of Montserrat in the Lesser Antilles. Vertebrate remains provide evidence for the use of both terrestrial and marine resources. Fish were obtained primarily from banks or reefs rather than inshore or offshore waters. The terrestrial resources include animals introduced by humans and indigenous animals eventually driven to extinction as a result of human activities. The ratio of marine to terrestrial resources is similar to that reported for other Saladoid sites in the Lesser Antilles. Differences among Saladoid faunal collections from the Lesser Antilles suggest that people living on each island knew well how to make use of local animals and were not transient South Americans unfamiliar with the resources offered by Caribbean islands.

INTRODUCTION

In 1984 David W. Steadman, David R. Watters, Gregory K. Pregill, and Elizabeth J. Reitz (Steadman et al., 1984*b*) argued that analysis of archaeological faunal remains from Montserrat was important for several reasons. First, it could identify the indigenous fauna used by Saladoid colonizers during what appears to be the first human occupation of the island. Second, faunal identification could establish the contemporaneity of Caribbean peoples with species now extinct on Montserrat. Third, vertebrate remains could be compared to those found in pre-Columbian sites elsewhere in the West Indies, thereby providing information useful on a regional scale.

These contributions are related to several broad Caribbean issues. One of the most important of these is the character of the adaptation made by Saladoid peoples when they left the South American mainland to colonize islands whose vertebrate resources were unfamiliar. Within a broadly similar pattern, it appears likely that Saladoid immigrants developed strategies appropriate to the exploitation of those vertebrate resources found on each island colonized.

An important aspect of this adaptation is the role of terrestrial animals in subsistence efforts of Saladoid peoples as they colonized the island chain. Elizabeth Wing (1989) observed that remains of terrestrial mammals, pigeons, lizards, and crabs are most abundant in either deposits from the Greater Antilles or early deposits in the Lesser Antilles. Wing (1989) found that an average of 34% of the individuals in Greater Antilles faunal assemblages were terrestrial animals while 38% of the individuals in early Lesser Antilles faunal collections were terrestrial (Table 1). The two most common terrestrial animals were rice rats and hutias. In contrast, 19% of the individuals in faunal assemblages from late deposits in the Lesser Antilles and 17% of the individuals in deposits from the Bahamas were terrestrial. Ranges for the four categories overlap; and variations in sample size

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Submitted 1 November 1993.

Table 1.—*Terrestrial animals in the Lesser Antilles. Data from the Bahamas, Greater Antilles, and Early and Late sites from the Lesser Antilles from Wing (1989). Trants data from this paper, excluding Stratum A.*

		Average %MNI
Lesser Antilles		
	Early sites	38%
	Late sites	19%
Trants		
	1/4" samples	57%
	1/8" samples	44%

and recovery techniques limited the conclusions that could be drawn from these observations (Wing, 1989).

Extensive use of indigenous terrestrial animals at early sites is found in conjunction with evidence that colonists introduced South American animals such as opossum, guinea pig, agouti, and dog into the West Indies (Wing, 1989). This use of indigenous terrestrial fauna and transportation of exotic animals throughout the Caribbean system extended into the post-Columbian period. Its impact on the zoogeography of the Caribbean caused the extinction of many indigenous forms (Olson, 1978, 1982; Pregill and Olson, 1981; Olson and Pregill, 1982; Steadman et al., 1984a; Morgan and Woods, 1986; Woods, 1989, 1990). Extinctions were also probably an important factor in early human colonization of the Lesser Antilles (Keegan and Diamond, 1987).

This issue will be addressed using data from a Saladoid occupation at the Trants site (MS-G1) on Montserrat. The Trants vertebrate collection is relevant because the sample size is large and the recovery technique used during excavation was good. The faunal data provide evidence for the use of indigenous and exotic terrestrial animals at an early Ceramic Age site in the Lesser Antilles. The Trants data indicate that Saladoid colonists made use of the resources found on Montserrat in a way not suggested by faunal assemblages from elsewhere in the Lesser Antilles, but nonetheless consistent with the general Caribbean pattern described by Wing (1989).

MATERIALS AND METHODS

Trants is a large, pre-Columbian site located on the eastern, or windward, side of Montserrat, one of the northern Lesser Antilles (Fig. 1). Montserrat is a small island of volcanic origin and Trants is located on one of the largest sections of relatively flat land found on the island (Steadman et al., 1984b). Sandy beaches and shallow inshore waters are limited around Montserrat. The east coast of the island is characterized by rugged cliffs. These are found north of Trants Bay as well as south of Farm Bay (Fig. 2). The beach at Trants Bay, just north of the site, is composed of cobble but Farm Bay has a sandy beach. The site is roughly 400 m inland from a rocky portion of the coast between the two bays, about 300 m from Trants Bay and 600 m from Farm Bay (Fig. 2). A small water course, Farm River Ghaut, runs south of the site. Today the stream is interrupted by a dam, but in the past it probably was a permanent water course. The mouth of Farm River Ghaut may have formed one of the few estuaries on the island, and a mangrove swamp may also have been present in Farm Bay (Newsom, 1994). The waters of Montserrat contain more patch reefs than fringe reefs and they are mainly found on the north, west, and south of the island rather than near Trants. However, there are some small patch reefs and seagrass beds in the limited inshore area adjacent to Trants.

The specimens reported here were excavated from the Trants site (MS-G1) in 1979 by Watters and in 1990 by Watters and James B. Petersen (Petersen and Watters, 1991; Watters, 1994). In the discussion that follows, reference will be made to materials recovered from a 2 × 2 m excavation

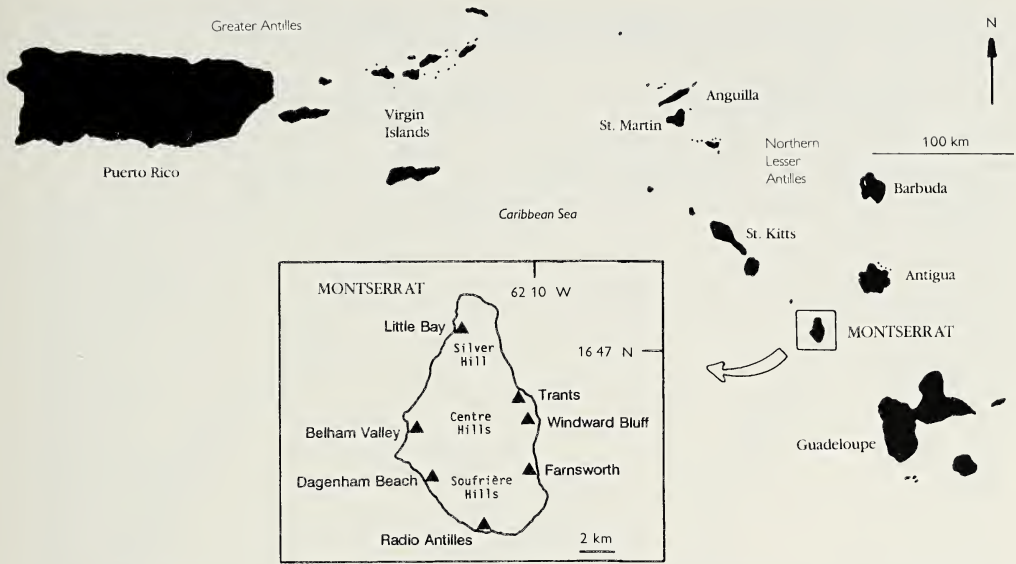


Fig. 1.—The Trants prehistoric site is located on the east coast of Montserrat in the northern Lesser Antilles.

unit (Test Pit 1) dug in the core area in 1979 (Steadman et al., 1984b). The 1979 excavation was in 10 cm increments and sediments were dry-screened through 1/8" mesh. These increments were combined into three analytical strata: Strata I(D), I, and II. Strata I and II were interpreted as Saladoid occupations. Vertebrates from Stratum I(D), the uppermost level, were not included in the calculations because of historic period disturbance.

The 1990 vertebrate remains are from three 1 × 1 m excavation units: N396E571, N421/22E645, and N596E571, all within the core area (Fig. 2). Each of the 1990 excavation units was dug in four quadrants. Faunal remains in three quadrants were collected in 1/4" mesh screens and in the fourth quadrant using 1/8" mesh screen. Some 1 mm window-screened samples were also collected, but time did not permit their study. In order to explore the impact of recovery techniques, vertebrate materials from the 1/4" quadrants are compared to those from the 1/8" quadrants. These are referred to as 1/4" samples and 1/8" samples.

The 10 cm-levels of the 1990 excavation units were combined into three analytical strata, two of which are associated with the Saladoid occupation. Stratum A is the historic hoe zone, Stratum B was deposited around A.D. 60–200, and Strata C and D were deposited around 480–10 B.C. (Petersen and Watters, 1991). Data from Stratum A are excluded from this analysis because historic and prehistoric artifacts were mixed in Stratum A. An Old World rat (*Rattus* sp.) was found in Feature 3, Unit 421/22E645 [Provenience Number (PN) 2027] which underlies Stratum A. Since *Rattus* clearly is a post-Columbian animal, it was necessary to exclude Feature 3 and all deposits above it to insure that only pre-Columbian vertebrate remains were studied. The Stratum D assemblage was so small that it was combined with samples from Stratum C. Although each of the strata from the three units may be from different time periods within the Saladoid occupation, or represent distinct activity areas within a large settlement, their temporal or social relationships have not been clarified. Data for each of the strata and units are presented separately, but are combined in the discussion. Other details of excavation are provided elsewhere (Petersen and Watters, 1991; Watters, 1994).

Faunal materials from the 1979 excavation were studied by several people. Birds and mammals were examined by Steadman, reptiles by Pregill, and fish by Reitz. All vertebrate materials recovered during the 1990 excavation were studied by Reitz using the comparative skeletal collections at the Florida Museum of Natural History and the University of Georgia Museum of Natural History. During the 1990 study, a record was made of the Number of Identified Specimens (NISP), the portion of each bone recovered, the bone's symmetry, and an estimate of age at death. Modifications to the bones (primarily burning) and weights were also recorded but are not presented here; these data are on file at the Georgia Museum of Natural History and are available upon request.

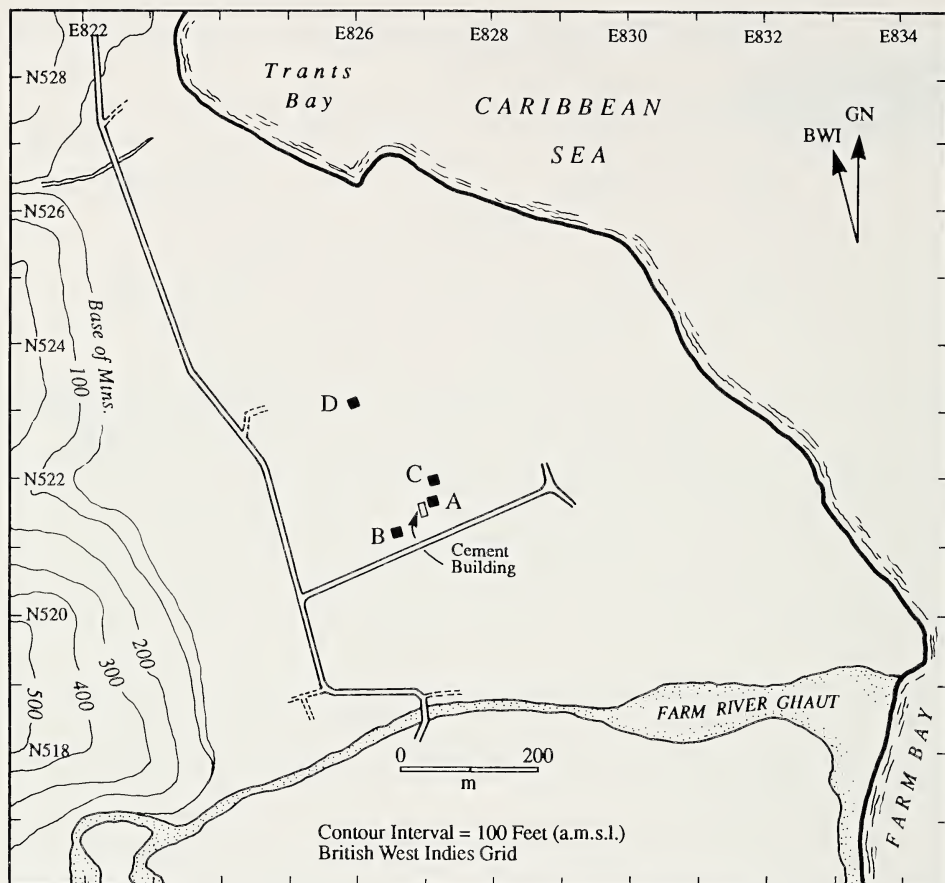


Fig. 2.—The Trants site with the excavation units noted using British West Indies grid (Watters, 1994). Unit A is the 1979 Test Pit 1, Unit B is N396E571, Unit C is N421/422E645, Unit D is N596E571. Excavation units are not to scale.

In order to estimate the Minimum Number of Individuals (MNI), samples from the three excavation units (N396E571, N421/22E645, and N596E571) were kept separate, as were samples from each of the three strata, creating nine analytical units. Because only a few elements could be identified to genus, a higher MNI estimate was sometimes obtained by family or tribe, than at the genus or species level. For example, more individuals might be estimated when *Oryzomyini*, *Oryzomyini* A, and *Oryzomyini* B were combined than when bones identified as *Oryzomyini* A or *Oryzomyini* B were counted independently. When that was the case, the estimates of MNI for lower taxonomic levels are included in the species lists in parentheses. Estimates included in parentheses are not included in the total for each list or in subsequent calculations.

Relative age of oryzomyines was estimated based on the degree of epiphyseal fusion for diagnostic elements. When animals are young their bones are not fully formed. Along the area of growth the shaft and the end of the bone, the epiphysis, are not fused. When growth is complete the shaft and epiphysis fuse. While environmental factors influence the actual age at which fusion is complete (Watson, 1978), elements fuse in a regular temporal sequence (e.g., Silver, 1963; Schmid, 1972; Gilbert, 1980). In most cases, one end of the bone fuses before the other. Bones were recorded as complete, proximal (p), or distal (d), and either fused (f) or unfused (unf). Hence a humerus recorded as "punfdf" would be unfused at the proximal end and fused at the distal end.

Age was estimated for oryzomyines based on toothwear. The criteria defined by Wing (1993b) were applied to those teeth still in the maxilla or mandible. Teeth in Stage 1 are unworn molars, stage 2 is

Table 2.—Bone count (NISP) and Minimum Number of Individuals (MNI) from N396E571, Trants, Montserrat, by stratum (A, B or C/D) and recovery technique.

Taxon	N396E571 ¼" samples						N396E571 ½" samples					
	Stratum						Stratum					
	A		B		C/D		A		B		C/D	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
UID fish	3		39		33		76		274		51	
Serranidae	1	1			1				2			
<i>Epinephelus</i> sp.			1	1	5	1	2	1	3	1		
<i>Mycteroperca</i> sp.			1	1			1	1	6	6		
Carangidae			2	1			3	1	2			
<i>Caranx</i> sp.											1	1
<i>Selene</i> sp.									1	1		
Lutjanidae			1	1	1	1						
Haemulidae			1	1			1	1				
Sparidae									2	1		
<i>Bodianus rufus</i>			2	1	1	1						
<i>Halichoeres</i> sp.							1	1	1	1		
Scaridae									1	1		
<i>Sparisoma</i> sp.			1	1			1	1				
Scombridae	1	1					1	1				
Balistidae			1	1	1	1			3	1		
UID turtle	1	1	3	1								
Cheloniidae									1	1		
UID lizard							3		1			
<i>Iguana</i> sp.							1	1	14	1	2	1
Colubridae					1	1	3	1	8	1	2	1
UID bird									12		3	
Columbidae			3	1	2	1			2	1		
Passeriformes							1	1	1	1	1	1
UID mammal	2	1	1				1		80		6	
cf. <i>Oryzomyini</i>			2	1	2	1	15		22			
<i>Oryzomyini</i>							15	4	47	3	1	1
<i>Oryzomyini</i> A							5	(3)	3	(1)		
<i>Oryzomyini</i> B							1	(1)	2	(2)		
<i>Dasyprocta aguti</i>							4	1				
<i>Canis familiaris</i>			3	1					12	1	2	1
Totals	8	4	61	12	47	7	135	15	500	21	69	6

characterized by slight wear on the tips of the cusps, stage 3 teeth are substantially worn, and teeth classified as Stage 4 were worn to the point that the tooth surface was flat and the dentine entirely exposed. Animals with toothwear classified as Stages 1 or 2 are considered juveniles and those with toothwear in Stages 3 or 4 are referred to as adults. As with fusion, environmental variables, especially type of forage, are known to influence the rate of wear (Grant, 1978).

Measurements of bones were taken where preservation allowed. In the case of birds and mammals, these measurements followed the guidelines established by Driesch (1976). Additionally, the anterior width of the centrum of the fish atlas and the alveolar length (AL) of oryzomyine mandibles and maxilla were recorded. Ideally only completely fused bones would be measured; however, oryzomyines typically do not live long enough for many bones to fuse. Consequently, greatest length (GL) was taken of unfused but otherwise complete humerus, femur, tibia, and calcaneus diaphyses. These exceptions are noted with the measurements. These measurements represent animals that had not attained full maturity and represent the size/age of individuals in that portion of the oryzomyine population exploited by people at Trants. This procedure permits comparison of the Trants oryzomyine data with those reported by Wing (1993b).

The species identified are summarized by four faunal categories based on vertebrate class and habitat preferences: Terrestrial, Inshore, Reef, and Pelagic. All mammals, birds, and reptiles were classified

Table 3.—Bone count (NISP) and Minimum Number of Individuals (MNI) from N421/22E645, Trants, Montserrat, by stratum (A, B, or C/D) and recovery technique.

Taxon	N421/22E645 ¼" samples						N421/22E645 ⅛" samples					
	Stratum						Stratum					
	A		B		C/D		A		B		C/D	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
UID fish	146		10		189		535		10		272	
<i>Tylosaurus</i> sp.							1	1				
Serranidae	1						1				6	
<i>Epinephelus</i> sp.	18	2			40	3	10	3			24	3
<i>Mycteroperca</i> sp.	1	1					9	8			2	1
Carangidae	2	1							1	1		
<i>Trachinotus goodei</i>							1	1				
Lutjanidae	1											
<i>Lutjanus</i> sp.	1	1										
Haemulidae							1	1			1	
<i>Anisotremus</i> sp.	1	1									1	1
<i>Haemulon</i> sp.											1	1
Labridae											1	1
<i>Bodianus rufus</i>	1	1	1	1			1	1				
<i>Halichoeres</i> sp.	5	2			9	2	2	1				
Scaridae							1					
<i>Scarus</i> sp.							1	1				
<i>Sparisoma</i> sp.	2	1	1	1								
Balistidae	3	1					87	1			2	1
UID reptile							4					
UID turtle	25						8	1				
Cheloniidae	6	1			1	1						
UID lizard	2						4				9	
<i>Iguana</i> sp.	11	1	1	1	21	3	22	1			18	2
Teiidae					1						3	1
<i>Ameiva</i> sp.					3	1	2	1				
Colubridae					1	1	6	1				
UID bird	14		1		58		37				28	
Columbidae	18	2	3	1	37	4	6	1			8	1
Passeriformes					32	8	4	1			16	3
UID mammal	8		3		2		9					
UID large mammal	8				1							
cf. <i>Oryzomyini</i>	21		1	1	10		112		1	1	19	
<i>Oryzomyini</i>	66	7			10	3	17	3			31	3
<i>Oryzomyini</i> A	1	(1)			3	(1)	11	(2)				
<i>Oryzomyini</i> B	13	(2)			6	(2)	15	(1)				
<i>Rattus</i> sp.							1	1				
<i>Dasyprocta aguti</i>	2	1					5	1				
<i>Canis familiaris</i>	1	1			1	1						
Totals	378	24	21	5	425	27	913	29	12	2	442	18

as Terrestrial, including ducks, rails, and sea turtles. These animals are closely associated with inshore waters and their capture might have been from either land or sea. In placing them in the Terrestrial category preference in capture technique is given to capture of nesting animals. Inshore taxa include sharks, palometa, porgies, drums, and gobies. The only pelagic fishes were mackerels. All other fishes were classified as reef inhabitants. Some, if not all, of these animals might be found in other habitats, either occasionally or because one or two members of the family occupy another habitat routinely. In these cases, classification reflects the location most members of each family commonly frequent and hence the most likely habitat in which they would have been captured, although this is not the only habitat that might have been exploited.

Table 4.—Bone count (NISP) and Minimum Number of Individuals (MNI) from N596E571, Trants, Montserrat, by stratum (A, B or C/D) and recovery technique.

Taxon	N596E571 ¼" samples						N596E571 ½" samples					
	Stratum						Stratum					
	A		B		C/D		A		B		C/D	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
<i>Ginglymostoma cirratum</i>			1	1								
Carcharhinidae									1	1		
UID fish	66		315		31		251		802		68	
Serranidae	1		5									
<i>Diplectrum</i> sp.							1	1				
<i>Epinephelus</i> sp.	4	1	47	4	2	1	4	2	23	4	1	1
<i>Mycteroperca</i> sp.	1	1	1	1			1	1	9	8	2	1
Carangidae			1	1	1	1	1	1	4		1	1
<i>Caranx</i> sp.									4	1		
<i>Trachinotus goodei</i>									2	2		
Lutjanidae			6	2	1	1			1			
<i>Lutjanus</i> sp.	4	1							5	1		
<i>Ocyurus chrysurus</i>											2	1
Haemulidae			2						1			
<i>Anisotremus</i> sp.			2	2					1	1		
<i>Conodon nobilis</i>							1	1				
<i>Haemulon</i> sp.			3	1			1	1				
Sciaenidae									1	1		
<i>Bodianus rufus</i>			1	1								
<i>Halichoeres</i> sp.	1	1	3	1					7	2		
<i>Sparisoma</i> sp.	1	1										
Gobiidae									1	1		
Scombridae	1	1							1	1		
Balistidae									4	1		
UID turtle			1									
Cheloniidae	16	1	44	1					8	1		
UID lizard							12		33		3	
<i>Iguana</i> sp.	11	1	85	3	15	1	2	1	32	1		
Teiidae									2	2		
<i>Ameiva</i> sp.							1	1	1	(1)	1	1
Colubridae			1	1			2	1	18	1	1	1
UID bird			23		4		9		32		3	
Anatidae			1	1					1	1		
Rallidae			2	1								
Columbidae	4	2	18	3	3	1	5	1	7	4	1	1
Passeriformes	1	1	7	2	2	1	6	1	24	2	3	1
UID mammal	4		3						1			
cf. <i>Oryzomyini</i>	3	1					16		17			
<i>Oryzomyini</i>			2	1			1	1				
<i>Oryzomyini</i> A			1	(1)					1	1		
<i>Oryzomyini</i> B									1	1		
<i>Dasyprocta aguti</i>							1	1				
Totals	118	12	575	27	59	6	315	14	1045	38	86	8

RESULTS

Vertebrate remains in the samples from the three Trants excavation units indicate that both terrestrial and marine resources were used by residents (Tables 2–4). In general, similar resources were present in all three units. The highest percentages were from the Terrestrial and Reef categories. Animals from inshore

waters were very rare and offshore conditions were represented by a single individual.

In each unit, Terrestrial vertebrates were more common in Stratum C/D than in Stratum B. The frequency of Terrestrial vertebrates ranged from 50% to 71% in Stratum C/D and from 39% to 57% in Stratum B. Terrestrial individuals were least common in Unit N396E571, Stratum B (Table 2) with 39% of the individuals; 12% of the individuals were rice rats and 9% were pigeons (Columbidae) and passerine birds (Passeriformes). Terrestrial individuals were most common in Unit N421/22E645, Stratum C/D (Table 3), representing 71% of the individuals; 13% of the individuals were rice rats (Oryzomyini) and 36% were pigeons and passerine birds. Oryzomyines occurred in all strata of all units, with the exception of Stratum C/D in Unit N596E571 (Table 4), which contained no mammals at all. Although terrestrial resources contributed 50% of the individuals in the sample from that stratum, these were exclusively lizards, a snake, pigeons, and passerine birds.

The samples from the quadrants recovered using $\frac{1}{4}$ " and $\frac{1}{8}$ " mesh were similar, at least in terms of MNI (Tables 5, 6). The $\frac{1}{4}$ " component contained 32 identified taxa, and the $\frac{1}{8}$ " component contained 39 taxa, although the latter component contained almost twice as many bones (Table 5). Terrestrial habitats contributed 57% of the individuals in the $\frac{1}{4}$ " fraction and 44% in the $\frac{1}{8}$ " samples (Table 6). Oryzomyine rodents were present in both components in roughly equal numbers, as were reptiles. Pigeons and passerines were more common in the $\frac{1}{4}$ " samples, whereas fish individuals were more common in the $\frac{1}{8}$ " samples. The difference between $\frac{1}{4}$ " and $\frac{1}{8}$ " recovery techniques is more clear when the measurements are examined (Table 7). Although grouper individuals of the genus *Epinephelus* were more common than those in the genus *Mycteroperca* in the $\frac{1}{4}$ " samples, the reverse was true in the $\frac{1}{8}$ " samples (Table 5). Significantly, *Mycteroperca* individuals are much smaller than the *Epinephelus* individuals (Table 7), which is why they were recovered primarily with the smaller-meshed screen. These two distinct sizes suggest that distinct fishing strategies were used in the capture of these two grouper genera, an observation that would not have been known if only the $\frac{1}{4}$ " samples had been studied. Since the materials recovered in the $\frac{1}{8}$ " mesh appear to be more representative of subsistence strategies at Trants, the following comments will be based on percentages from the $\frac{1}{8}$ " component only.

Fifty-six percent of the Trants individuals in the $\frac{1}{8}$ " component are sharks and bony fishes (Table 6). Most of the identifications could not be made to the specific level, hence the exact nature of the habitats from which these fish were taken is uncertain. Some species, such as the nurse shark (*Ginglymostoma cirratum*) are very common inshore, especially over rocky reefs and sand flats (Randall, 1968: 9). The palometa (*Trachinotus goodei*), porgy (Sparidae), drum (Sciaenidae), and goby (Gobiidae) are also generally inshore fishes (Randall, 1968:114, 141, 149, 247). Other fishes are generally associated with coral reefs or rocky bottoms (Randall, 1968:57, 102, 121, 128, 199, 217). These include groupers (Serranidae, *Epinephelus* sp., *Mycteroperca* sp., jacks (Carangidae, *Caranx* sp., *Selene* sp.), snappers (Lutjanidae, *Lutjanus* sp., *Ocyurus chrysurus*), grunts (Haemulidae, *Anisotremus* sp., *Haemulon* sp.), wrasses (Labridae, *Bodianus rufus*, *Halichoeres* sp.), and parrotfishes (Scaridae, *Sparisoma* sp.). Groupers are the most abundant fish family in the Trants collection, constituting 28% of the individuals in the $\frac{1}{8}$ " component, and indicating that rocky outcrops were commonly fished. In contrast, wrasses and parrotfishes, characteristic of reefs, constituted only 4% of the indi-

viduals in the $\frac{1}{8}$ " samples. The only evidence that offshore waters were exploited is a single mackerel (Scombridae), which might have been taken as it swam over a bank or reef. This pelagic species contributed 1% of the individuals in the $\frac{1}{8}$ " fraction.

All reptiles were classified as Terrestrial vertebrates. Sea turtles (Cheloniidae) are not abundant in the Trants collection, constituting only 2% of the individuals in the $\frac{1}{8}$ " component. The individuals appear to be adults. Their scarcity probably reflects the rarity of sandy beaches for nesting on Montserrat. The east coast of the island is primarily composed of cobbles; however, Farm Bay is one of the east coast's few sandy beaches (Fig. 2) and one of the island's few seagrass beds (Eastern Caribbean Natural Area Management Program, 1980). While the classification of these turtles as Terrestrial suggests they were taken while nesting, it is also possible they were taken from the seagrass bed. The other reptiles were more clearly Terrestrial. These included iguanas (*Iguana* cf. *iguana*) and ameiva lizards (*Ameiva* cf. *pluvianotata*). Although not common on the island today, iguanas contribute 6% of the individuals in the $\frac{1}{8}$ " component. Colubrid snakes (Colubridae) were almost as common (4% of the MNI).

Among birds, ducks and rails might be considered Inshore rather than Terrestrial resources since they could have been taken from a bay or the Farm River Ghaut. The two largest groups of birds, however, were clearly Terrestrial. These included pigeons (Columbidae) and small passerine birds (Passeriformes). Pigeons contributed 8% of the individuals in the $\frac{1}{8}$ " component and native pigeons still survive on the island in spite of recent habitat destruction. The passerine order, which includes thrashers and finches, constituted 9% of the Trants individuals.

Eleven of the rodents in the pre-Columbian assemblage were rice rats (Oryzomyini), and an additional four were probably Oryzomyini (Table 5). Rice rats constitute 9% of the individuals in the samples recovered using $\frac{1}{8}$ " mesh (Table 6). Two species of rice rats were present on the island. Remains were found in all three excavation units and in most of the strata, but they were most common in Stratum A, particularly in Unit N421/22E645 (Table 3), suggesting that both large and small rice rats may have survived into the post-Columbian period. They were probably driven to extinction by humans in combination with cats, dogs, and Old World rodents introduced in the recent past.

Although most of the specimens could only be identified as unidentified (UID) rodent or oryzomyine, the measurements (Table 7) suggest that there were at least two species (Fig. 3). Steadman found two species of oryzomyines in his study of the 1979 Trants vertebrate remains (Steadman et al., 1984b). He classified these as a small oryzomyine, Undescribed Species A, and a large oryzomyine, Undescribed Species B, and this distinction is followed here. At least four of the Oryzomyini individuals were the small rice rat, (Oryzomyini A), and at least five of the individuals were the large rice rat (Oryzomyini B) (Table 5). The size differences probably do not reflect simply younger versus older individuals since the alveolar lengths (Table 7) support the presence of two distinct sizes of rice rats rather than differences in maturation. The average alveolar length of the small oryzomyine mandible is 7.08 mm ($n = 3$) and the average alveolar length of the large oryzomyine mandible is 10.09 mm ($n = 4$) (Table 7). Allometric correlations between the width of the femur head and body weight (Wing and Brown, 1979: 127–129) predict an average weight of 181 g for the smaller West Indian rice rats and up to 300 g for the larger ones (Wing, 1993a). Degree of fusion (Table 7) and toothwear (Table 8) indicate that most of the rice rats in Strata B and C/D were

Table 5.—Bone count (NISP) and Minimum Number of Individuals (MNI) for $\frac{1}{4}$ " samples and $\frac{1}{8}$ " samples with Stratum A excluded and Strata B and C/D combined, Trants, Montserrat. All three units are combined.

Taxon	$\frac{1}{4}$ " Samples		$\frac{1}{8}$ " Samples	
	NISP	MNI	NISP	MNI
Sharks				
<i>Ginglymostoma cirratum</i>	1	1		
Nurse shark				
Carcharhinidae			1	1
Requiem sharks				
Fishes				
UID fish	617		1477	
Serranidae	6		8	
Sea basses				
<i>Epinephelus</i> sp.	95	10	51	9
Grouper				
<i>Mycteroperca</i> sp.	2	2	19	16
Grouper				
Carangidae	4	3	8	2
Jacks				
<i>Caranx</i> sp.			5	2
Jack				
<i>Selene</i> sp.			1	1
Lookdown				
<i>Trachinotus goodei</i>			2	2
Palometa				
Lutjanidae	9	5	1	
Snappers				
<i>Lutjanus</i> sp.			5	1
Snapper				
<i>Ocyurus chrysurus</i>			2	1
Yellowtail snapper				
Haemulidae	3	1	2	
Grunts				
<i>Anisotremus</i> sp.	2	2	2	2
Margate				
<i>Haemulon</i> sp.	3	1	1	1
Grunt				
Sparidae			2	1
Porgies				
Sciaenidae			1	1
Drums				
Labridae			1	1
Wrasses				
<i>Bodianus rufus</i>	5	4		
Spanish hogfish				
<i>Halichoeres</i> sp.	12	3	8	3
Wrasse				
Scaridae			1	1
Parrotfishes				
<i>Sparisoma</i> sp.	2	2		
Parrotfish				
Gobiidae			1	1
Gobies				
Scombridae			1	1
Mackerels				
Balistidae	2	2	9	3
Leatherjackets				

Table 5.—*Continued.*

Taxon	$\frac{1}{4}$ " Samples		$\frac{1}{8}$ " Samples	
	NISP	MNI	NISP	MNI
Reptiles				
UID turtle	4	1		
Cheloniidae	45	2	9	2
Sea turtles				
UID lizard			46	
<i>Iguana</i> sp.	122	8	66	5
Iguana				
Teiidae	1		5	3
Whiptails				
<i>Ameiva</i> sp.	3	1	2	(2)
Ameiva lizard				
Colubridae	3	3	29	4
Non-poisonous snakes				
Birds				
UID bird	86		78	
Anatidae	1	1	1	1
Ducks				
Rallidae	2	1		
Rails				
Columbidae	66	11	18	7
Pigeons and doves				
Passeriformes	41	11	45	8
Song birds				
Mammals				
UID mammal	9		87	
UID large mammal	1			
UID rodent	15	3	59	1
Oryzomyini	12	4	79	7
Rice rat				
Oryzomyini A	4	(2)	4	(2)
Small rice rat				
Oryzomyini B	6	(2)	3	(3)
Large rice rat				
<i>Canis familiaris</i>	4	2	14	2
Dog				
UID vertebrate				
Totals	1188	84	2154	90

Table 6.—*Summary table of vertebrate fauna from Trants, Montserrat.*

	$\frac{1}{4}$ " Samples		$\frac{1}{8}$ " Samples	
	MNI	%MNI	MNI	%MNI
Sharks/fishes	36	42.9	50	55.6
Reptiles	15	17.9	14	15.6
Pigeons/passerines	22	26.2	15	16.7
Other birds	2	2.4	1	1.1
Oryzomyine rodents	7	8.3	8	8.9
Dog	2	2.4	2	2.2
Totals	84		90	

Table 7.—Measurements of vertebrate bones from Trants, Montserrat, in mm. Measurement dimensions follow Driesch (1976). PN refers to provenience number and stratum to level.

Taxon	Element	Dimension	Measure- ment	Fusion	PN	Stratum
<i>Ginglymostoma cirratum</i>	vertebra	width	9.80		2214	B
<i>Tylosaurus</i> sp.	atlas	width	4.50		2020	A
<i>Epinephelus</i> sp.	atlas	width	2.35		2033	A
<i>Epinephelus</i> sp.	atlas	width	2.80		1913	A
<i>Epinephelus</i> sp.	atlas	width	2.80		1926	B
<i>Epinephelus</i> sp.	atlas	width	3.80		2024	A
<i>Epinephelus</i> sp.	atlas	width	5.96		2019	A
<i>Epinephelus</i> sp.	atlas	width	6.73		1959	A
<i>Epinephelus</i> sp.	atlas	width	6.81		1939	C
<i>Epinephelus</i> sp.	atlas	width	7.05		2050	A
<i>Epinephelus</i> sp.	atlas	width	7.29		2215	B
<i>Mycteroperca</i> sp.	atlas	width	1.70		2220	C
<i>Mycteroperca</i> sp.	atlas	width	1.80		2209	B
<i>Mycteroperca</i> sp.	atlas	width	1.90		1926	B
<i>Mycteroperca</i> sp.	atlas	width	1.90		1926	B
<i>Mycteroperca</i> sp.	atlas	width	1.95		2100	C
<i>Mycteroperca</i> sp.	atlas	width	2.00		1913	A
<i>Mycteroperca</i> sp.	atlas	width	2.02		2032	A
<i>Mycteroperca</i> sp.	atlas	width	2.10		1964	A
<i>Mycteroperca</i> sp.	atlas	width	2.10		1980	B
<i>Mycteroperca</i> sp.	atlas	width	2.10		1980	B
<i>Mycteroperca</i> sp.	atlas	width	2.10		1980	B
<i>Mycteroperca</i> sp.	atlas	width	2.10		2020	A
<i>Mycteroperca</i> sp.	atlas	width	2.10		2020	A
<i>Mycteroperca</i> sp.	atlas	width	2.20		2020	A
<i>Mycteroperca</i> sp.	atlas	width	2.20		2027	A
<i>Mycteroperca</i> sp.	atlas	width	2.30		1921	B
<i>Mycteroperca</i> sp.	atlas	width	2.30		2024	A
<i>Mycteroperca</i> sp.	atlas	width	2.40		1937	B
<i>Mycteroperca</i> sp.	atlas	width	2.40		2209	B
<i>Mycteroperca</i> sp.	atlas	width	2.50		1926	B
<i>Mycteroperca</i> sp.	atlas	width	2.56		1934	B
<i>Mycteroperca</i> sp.	atlas	width	2.60		1980	B
<i>Mycteroperca</i> sp.	atlas	width	2.60		1980	B
<i>Mycteroperca</i> sp.	atlas	width	2.67		2206	B
<i>Mycteroperca</i> sp.	atlas	width	2.90		2020	A
<i>Mycteroperca</i> sp.	atlas	width	3.20		2027	A
Carangidae	atlas	width	2.80		1909	A
<i>Caranx</i> sp.	atlas	width	2.00		1947	C
<i>Selene</i> sp.	atlas	width	3.60		1917	B
<i>Trachinotus goodei</i>	atlas	width	2.20		2209	B
<i>Trachinotus goodei</i>	atlas	width	3.40		2209	B
<i>Lutjanus</i> sp.	atlas	width	5.69		1928	B
<i>Ocyurus chrysurus</i>	atlas	width	1.40		2220	C
<i>Sparisoma</i> sp.	atlas	width	5.41		1966	A
Gobiidae	atlas	width	1.12		2209	B
Anatidae	carpometacarpus	Bp	11.80		1984	B
Anatidae	carpometacarpus	Did	5.80		1984	B
Anatidae	carpometacarpus	GL	52.20		1984	B
Rallidae	humerus	Bd	7.30		1993	B
Rallidae	humerus	Bp	10.00		1993	B
Rallidae	humerus	GL	46.50		1993	B
Rallidae	tibiotarsus	Bd	5.30		1993	B
Rallidae	tibiotarsus	Dd	5.60		1993	B
Columbidae	carpometacarpus	Bp	7.00		1984	B
Columbidae	carpometacarpus	Bp	7.20		1980	B

Table 7.—Continued.

Taxon	Element	Dimension	Measurement	Fusion	PN	Stratum
Columbidae	carpometacarpus	Bp	7.40		2072	C
Columbidae	carpometacarpus	Bp	7.90		1974	B
Columbidae	carpometacarpus	Bp	8.00		2055	A
Columbidae	carpometacarpus	Bp	8.20		1976	B
Columbidae	carpometacarpus	Bp	9.90		2072	C
Columbidae	carpometacarpus	Did	4.20		2020	A
Columbidae	carpometacarpus	Did	4.30		1984	B
Columbidae	carpometacarpus	Did	4.80		1974	B
Columbidae	carpometacarpus	Did	4.80		1980	B
Columbidae	carpometacarpus	Did	5.20		2072	C
Columbidae	carpometacarpus	Did	5.40		2029	A
Columbidae	carpometacarpus	Did	6.90		2066	C
Columbidae	carpometacarpus	GL	24.60		1984	B
Columbidae	carpometacarpus	GL	24.90		1980	B
Columbidae	carpometacarpus	GL	26.50		1974	B
Columbidae	coracoid	Lm	27.00		1972	A
Columbidae	coracoid	Lm	31.40		1971	A
Columbidae	coracoid	Lm	31.50		2066	C
Columbidae	coracoid	Lm	32.70		2042	C
Columbidae	coracoid	Lm	34.90		2072	C
Columbidae	coracoid	Lm	35.80		2066	C
Columbidae	coracoid	Lm	36.80		2072	C
Columbidae	femur	Bd	7.20		2064	B
Columbidae	femur	Bd	7.30		2072	C
Columbidae	femur	Bd	7.80		2041	C
Columbidae	femur	Bp	7.10		1984	B
Columbidae	femur	Bp	7.20		2223	C
Columbidae	femur	Bp	7.40		2020	A
Columbidae	femur	Bp	7.50		2072	C
Columbidae	femur	Bp	8.50		1926	B
Columbidae	femur	Dd	5.50		2064	B
Columbidae	femur	Dd	6.00		2072	C
Columbidae	femur	Dd	6.50		2041	C
Columbidae	femur	Dp	4.10		1984	B
Columbidae	femur	Dp	4.40		2020	A
Columbidae	femur	Dp	4.70		2072	C
Columbidae	humerus	Bd	7.90		1941	C
Columbidae	humerus	Bd	7.90		1972	A
Columbidae	humerus	Bd	8.10		2022	A
Columbidae	humerus	Bd	8.50		2066	C
Columbidae	humerus	Bd	9.20		1984	B
Columbidae	humerus	Bd	9.20		2203	B
Columbidae	humerus	Bd	9.50		1961	A
Columbidae	humerus	Bd	9.50		1972	A
Columbidae	humerus	Bd	9.50		2024	A
Columbidae	humerus	Bd	12.50		2085	C
Columbidae	humerus	Bp	13.10		2041	C
Columbidae	humerus	Dip	13.10		1972	A
Columbidae	humerus	GL	39.50		1972	A
Columbidae	radius	Bd	5.00		2066	C
Columbidae	radius	Bd	5.50		2072	C
Columbidae	radius	GL	53.90		2066	C
Columbidae	scapula	Dic	6.40		1980	B
Columbidae	scapula	Dic	6.90		1980	B
Columbidae	scapula	Dic	7.00		1980	B
Columbidae	scapula	Dic	7.40		1980	B
Columbidae	scapula	Dic	7.50		1980	B

Table 7.—*Continued.*

Taxon	Element	Dimension	Measurement	Fusion	PN	Stratum
Columbidae	scapula	Dic	7.70		2203	B
Columbidae	scapula	Dic	7.80		2220	C
Columbidae	scapula	Dic	7.90		2201	B
Columbidae	scapula	Dic	8.10		2042	C
Columbidae	scapula	Dic	9.50		2042	C
Columbidae	scapula	Dic	9.70		2072	C
Columbidae	tarsometatarsus	Bd	6.80		2061	B
Columbidae	tarsometatarsus	Bd	7.00		2231	D
Columbidae	tarsometatarsus	Bd	7.40		2041	C
Columbidae	tarsometatarsus	Bp	6.50		2061	B
Columbidae	tarsometatarsus	GL	33.50		2061	B
Columbidae	tibiotarsus	Bd	5.10		1971	A
Columbidae	tibiotarsus	Bd	5.70		2020	A
Columbidae	tibiotarsus	Bd	5.70		2024	A
Columbidae	tibiotarsus	Bd	5.80		2017	A
Columbidae	tibiotarsus	Bd	6.80		2066	C
Columbidae	tibiotarsus	Bd	7.40		2066	C
Columbidae	tibiotarsus	Dd	4.80		1971	A
Columbidae	tibiotarsus	Dd	5.50		2017	A
Columbidae	tibiotarsus	Dd	5.50		2024	A
Columbidae	tibiotarsus	Dd	6.00		2020	A
Columbidae	tibiotarsus	Dd	6.50		2066	C
Columbidae	tibiotarsus	Dd	6.70		2066	C
Columbidae	tibiotarsus	Dip	8.90		2072	C
Columbidae	tibiotarsus	Dip	9.30		2041	C
Columbidae	ulna	Bp	5.50		2042	C
Columbidae	ulna	Bp	7.20		2041	C
Columbidae	ulna	Did	5.10		2029	A
Columbidae	ulna	Did	5.30		2021	A
Columbidae	ulna	Did	6.40		2102	C
Columbidae	ulna	Did	7.20		2072	C
Columbidae	ulna	Dip	7.20		2042	C
Columbidae	ulna	Dip	9.80		2041	C
Columbidae	ulna	GL	57.00		2041	C
Oryzomyini	femur	DC	4.10	pfdunf	2201	B
Oryzomyini	femur	DC	4.50	pf	1926	B
Oryzomyini	femur	DC	4.60	pf	1917	B
Oryzomyini	femur	DC	4.90	pfdunf	2114	C
Oryzomyini	femur	GL	34.80	pfdunf	2201	B
Oryzomyini	femur	GL	44.20	pfdunf	2114	C
Oryzomyini	humerus	GL	28.80	punfdf	2072	C
Oryzomyini	humerus	GL	29.40	punfdf	2020	A
Oryzomyini	humerus	GL	31.20	punfdf	2020	A
Oryzomyini	humerus	GL	31.70	punfdf	2020	A
Oryzomyini	mandible	AL	8.54		1974	B
Oryzomyini	mandible	AL	9.27		2042	C
Oryzomyini	mandible	AL	9.55		2041	C
Oryzomyini	mandible	AL	9.60		2042	C
Oryzomyini	mandible	AL	9.70		2041	C
Oryzomyini	mandible	AL	10.87		2051	A
Oryzomyini	maxilla	AL	8.78		2052	A
Oryzomyini	maxilla	AL	9.29		2053	A
Oryzomyini	maxilla	AL	9.53		2041	C
Oryzomyini	maxilla	AL	9.53		2041	C
Oryzomyini	maxilla	AL	9.53		2041	C
Oryzomyini	maxilla	AL	9.70		2029	A

Table 7.—Continued.

Taxon	Element	Dimension	Measurement	Fusion	PN	Stratum
Oryzomyini	maxilla	AL	9.80		2027	A
Oryzomyini	maxilla	AL	9.90		2020	A
Oryzomyini	maxilla	AL	9.92		2041	C
Oryzomyini A	astragalus	GL	4.00		1917	B
Oryzomyini A	astragalus	GL	4.20		2027	A
Oryzomyini A	astragalus	GL	4.50		1913	A
Oryzomyini A	astragalus	GL	4.80		1909	A
Oryzomyini A	astragalus	GL	4.80		1909	A
Oryzomyini A	astragalus	GL	5.81		2032	A
Oryzomyini A	calcaneus	GL	6.37	punf	2029	A
Oryzomyini A	femur	DC	3.20	pf	2066	C
Oryzomyini A	humerus	GL	21.70	punfdf	2066	C
Oryzomyini A	mandible	AL	7.00		2022	A
Oryzomyini A	mandible	AL	7.20		2209	B
Oryzomyini A	mandible	AL	7.50		1984	B
Oryzomyini A	maxilla	AL	6.75		2025	A
Oryzomyini B	astragalus	GL	6.30		1909	A
Oryzomyini B	astragalus	GL	6.59		1926	B
Oryzomyini B	astragalus	GL	6.70		2018	A
Oryzomyini B	calcaneus	GL	8.03	pf	1980	B
Oryzomyini B	calcaneus	GL	11.49	pf	2029	A
Oryzomyini B	femur	DC	5.30	pfdunf	2066	C
Oryzomyini B	femur	DC	5.40	pfdunf	2087	C
Oryzomyini B	femur	GL	46.60	pfdunf	2066	C
Oryzomyini B	femur	GL	46.70	pfdunf	2087	C
Oryzomyini B	mandible	AL	9.77		2066	C
Oryzomyini B	mandible	AL	10.10		2019	A
Oryzomyini B	mandible	AL	10.10		2022	A
Oryzomyini B	mandible	AL	10.40		2021	A
Oryzomyini B	tibia	GL	45.10	punfdf	2066	C
Oryzomyini B	tibia	GL	46.70	punfdf	2066	C
<i>Dasyprocta aguti</i>	humerus	Bd	11.90		2053	A
<i>Dasyprocta aguti</i>	tibia	Bd	9.90		2018	A
<i>Canis familiaris</i>	maxilla	B	12.62		2052	A
<i>Canis familiaris</i>	maxilla	L	13.90		2052	A

juveniles. Before extinction, both species were endemic on Montserrat and elsewhere in the Lesser Antilles. The presence of both rice rats on the same island, however, is unusual. Although the habitats preferred by the rice rats are not known, at least some members of this group tolerate disturbed, brushy, or cleared habitats such as those around human habitations, from which they raid fields and stored foods (Wolfe, 1982; Nowak and Paradiso, 1983:572; Eisenberg, 1989:351).

None of the rice rat materials were found in combinations that suggested animals that died in situ with little post-mortem disturbance. It has been demonstrated in other contexts that rodents even smaller than these were consumed (Szuter, 1988, 1991). Element distributions are confused by the use of two different screen sizes and identifiability. Over a third (36%) of the rice rat bones were cranial fragments identified in the 1/8" meshed screen. Only 11 carpals or tarsals could be identified as rice rats, and all were from the 1/8" meshed fraction. The 1/8" mesh fraction itself, however, comprised only a quarter of the excavated area of each

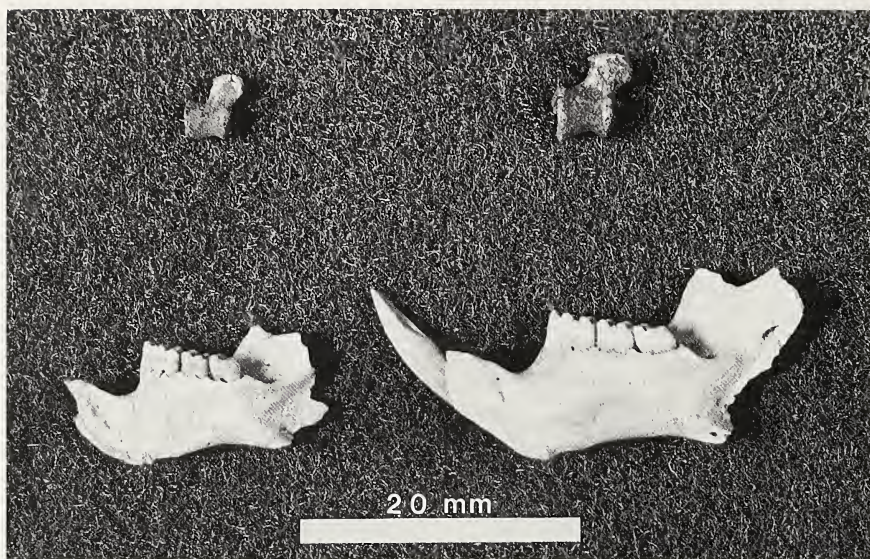


Fig. 3.—Astragali and mandible of oryzomyine A and oryzomyine B. The small astragalus and mandible are of oryzomyine A and the large elements are of oryzomyine B.

unit. No butchering marks were found on any of the Trants assemblage other than burning; 3% of the rice rat bones had been burned. There is no reason to assume these rice rats were not consumed, and the abundance of these animals in this assemblage and the absence of intact skeletons seems solid evidence that these fairly large rodents were eaten.

The land clearing and food storage associated with Saladoid peoples probably enhanced the resource base for rice rats on Montserrat. Wing (1993*b*) found that rice rats were extremely abundant in the Hope Estate faunal assemblage associated with a Saladoid occupation on the island of St. Martin. She anticipated that this level of use over a long period of time would result in overexploitation of rice rats. Based on data for a closely related rice rat (*Oryzomys palustris*) (Negus et al., 1961), she proposed that heavy human predation over time would result in a relative decrease in West Indian rice rat populations and a corresponding decrease of rice rats in human deposits. This might also be associated with a relatively heavy use of young animals as litter size increased in response to low population density (Negus et al., 1961). Wing (1993*b*) also predicted a decline in size as a consequence of selective predation upon larger rice rats.

The Trants oryzomyine materials were examined for evidence of overuse as proposed for Hope Estate. In the first place, rice rats constituted a much lower percentage of the individuals in the Trants collection than in that from Hope Estate. However, there was a decline in the percentage of oryzomyines from 11% of the individuals in Stratum C/D to 9% of the individuals in Stratum B. This decline in the usage of rice rats needs to be tested over a larger portion of the Trants site. If it is supported by additional stratigraphic analysis, then this may represent either a change in prey preference on the part of Saladoid residents or a decline in the island's rice rat population, or both.

In order to explore whether younger animals were exploited during more recent time periods, toothwear was compared among the three strata (Table 8). The

Table 8.—*Toothwear observed for oryzomyines, Trants, Montserrat. Wear stages as defined by Wing (1993b).*

Taxon	Element	Wear	Stratum
Oryzomyini	mandible	2	A
Oryzomyini	mandible	2	A
Oryzomyini	mandible	2.5	A
Oryzomyini B	mandible	2.5	A
Oryzomyini A	mandible	3	A
Oryzomyini B	mandible	3	A
Oryzomyini	mandible	3.5	A
Oryzomyini B	mandible	4	A
Oryzomyini A	mandible	2	B
Oryzomyini A	mandible	3	B
Oryzomyini	mandible	2	C
Oryzomyini	mandible	2	C
Oryzomyini	mandible	2	C
Oryzomyini	mandible	2	C
Oryzomyini B	mandible	2	C
Oryzomyini	maxilla	2	A
Oryzomyini	maxilla	3	A
Oryzomyini A	maxilla	3	A
Oryzomyini	maxilla	4	A
Oryzomyini	maxilla	4	A
Oryzomyini	maxilla	4	A
Oryzomyini B	maxilla	4	A
Oryzomyini	maxilla	2	C
Oryzomyini	maxilla	2	C
Oryzomyini	maxilla	2	C
Oryzomyini	maxilla	3	C

degree of toothwear in Strata C and B suggests that all individuals were juveniles. However, the oryzomyine mandibles and maxilla both indicate that those deposited in the lower strata were generally younger than those deposited in Stratum A. This suggests that rice rat population density during the Saladoid occupation was lower, perhaps due to greater predation compared to the post-Columbian period. Unfortunately, there were not sufficient measurements in each of the three strata to assess changes in body size through time. These data do suggest that rice rats were subject to overpredation during the Saladoid occupation of Trants compared to the post-Columbian occupation of the island, although data from contexts with better temporal definition are needed to explore this possibility further. The large number of older rice rats in Stratum A probably indicates that, at least during part of the time represented by the hoe zone, these were natural deaths in an unstressed population.

Terrestrial vertebrate resources also included two exotic forms introduced by humans. One of these is the agouti (*Dasyprocta aguti*). Steadman identified an agouti from Stratum 1(D) in the 1979 Trants fauna, a disturbed context. The 1990 sample contained 12 additional agouti bones, unfortunately also from disturbed contexts (Stratum A). The agouti was introduced from the South American mainland sometime in the pre-Columbian period. They are found in a number of archaeological deposits throughout the Lesser Antilles and until recently still lived on some of the islands (Nowak and Paradiso, 1983:816; Wing, 1989). They are still found on Montserrat and the presence of agouti bones in disturbed contexts

Table 9.—Comparison of resource use among several Saladoid vertebrate collections. Cayon data are from Wing (1989); Pearls data are from Stokes (1993); Trants ¼" data are from this paper; and Trants ⅛" data are from this paper (Trants ⅛") and from Test Pit 1 (Steadman et al., 1984b).

	Cayon		Pearls		Trants ¼"		Trants ⅛"		Test Pit 1	
	MNI	%MNI	MNI	%MNI	MNI	%MNI	MNI	%MNI	MNI	%MNI
Terrestrial	58	58.6	21	32.8	48	57.1	40	44.4	39	69.6
Inshore			14	21.9	1	1.2	6	6.7		
Reef	24	24.2	27	42.2	35	41.7	43	47.8	15	26.8
Pelagic	17	17.2	2	3.1			1	1.1	2	3.6
Totals	99		64		84		90		56	

may mean that they burrowed into the site or were buried in it quite recently. Therefore, it is not possible to confirm that these agouti remains are recent or Saladoid.

The remains of two dogs were identified in the ⅛" samples and two additional dogs were identified in the ¼" samples (Tables 2, 3). A subadult was found in Feature 2, Unit N396E571 (PN 1934, 1937) and the other three were individuals represented by bones too fragmentary to estimate age (PN 1923, 1929, 1935, 1943, 2087). Dogs are not endemic to the West Indies and probably accompanied humans during their migrations into the region. Since most dogs identified in the Caribbean have been recovered from burials rather than from middens (Wing, 1989), it is possible that they were valued companions rather than sources of food. However, the Trants dogs were not associated with burials nor were they articulated burials themselves.

DISCUSSION

The percentage of Terrestrial individuals puts the Trants assemblage above the average for early sites in the Lesser Antilles as calculated by Wing (1989; Table 1). Although sharks and bony fishes were the most common vertebrate group, birds and reptiles constituted a significant portion of the assemblage, with mammals somewhat less abundant.

Data from Trants indicate that people living on Montserrat made use of indigenous terrestrial fauna, exotic mammals, and marine animals. In this respect, Trants conforms to the general Caribbean pattern, in which most of the resources are from the nearest habitats (Wing, 1989). In the case of Trants, it appears that terrestrial and marine vertebrates were used in about equal numbers. Indigenous terrestrial fauna included rice rats, pigeons, passerine birds, and iguanas. Since this part of the Trants project focused on the vertebrate component, land crabs and mollusks are not included in this calculation; however, these were also very common in the collection (David Watters, personal communication, 1993). Some of the terrestrial resources were exotic animals introduced to the island from South America. As expected, marine resources in the Trants collection included sea turtles and fishes from banks, reefs, and offshore areas, with emphasis on those most accessible from the site.

Although these data support a general Saladoid pattern, they also indicate that a variety of subsistence strategies were practiced in the Lesser Antilles by Saladoid peoples, each one reflecting local conditions. Comparing the Trants materials to those from early sites on Grenada (Pearls) and St. Kitts (Cayon) (Wing, 1989; Stokes, 1993), the significance of adaptations to local conditions and the diversity

of subsistence strategies practiced in the Lesser Antilles by Saladoid peoples is clear (Table 9). The only mammal identified in all three collections was the dog. Both Trants and Pearls contained high percentages of oryzomyine rodents—17% of the individuals in the Pearls collection and 9% of the Trants $\frac{1}{8}$ " collection. By contrast, pigeons, so common in the Trants collection, were not identified in the Pearls assemblage. Iguana were found in all three collections; sea turtles, rare in the Trants collection, were not identified in the Cayon or Pearls collections.

Although the percentages of fish individuals from reefs and banks was similar between Pearls and Trants, there were differences among the kinds of fishes identified. For example, 28% of the individuals in the Trants collection (the $\frac{1}{8}$ " samples) are groupers, more typical of deeper waters, in contrast to 12% of the individuals in the Pearls collection. Wrasses and parrotfishes, typical of reefs, contributed 4% of the Trants $\frac{1}{8}$ " and 16% of the Pearls assemblages. Shallow water, inshore species, rare in the Trants collection, contributed almost a quarter of the Pearls individuals.

These differences probably reflect the types of marine habitats associated with each island. Shallow water areas are limited around Montserrat, which has more patch reefs than fringe reefs compared to islands such as Grenada and Barbuda. This leads to the conclusion that the subsistence strategy practiced at Trants is a local adaptation. It also suggests that it is probably not appropriate to develop models for the colonization of the Caribbean based on the assumption that Saladoid peoples everywhere made use of marine and terrestrial resources in the same way (Watters and Rouse, 1989).

One characteristic all three assemblages share is a high percentage of oryzomyine individuals, raising the question of whether rodents could support exploitation at these levels for a long period of time. (The hutia was introduced to Montserrat.) Consumption of rice rats increased between pre-horticultural and horticultural strata and then declined in later ones (Wing, 1993a). It may be that rice rats were consumed in limited amounts as a supplement to marine resources, iguanas, and land crabs before gardening began on those islands which were occupied during pre-horticultural periods. Use of rice rats and other garden pests may then have increased in levels associated with horticulture. Human horticultural activities could have contributed to an increase in rice rat population size because these plots provided optimum habitat for them. Rice rats could have been both a terrestrial mammalian meat source for Saladoid peoples as well as pests attracted by gardens and stored foods. Saladoid colonists may not have intentionally sought out rice rats, but rather taken advantage of a resource that essentially came to them, much as the garden hunting model suggested by Linares (1976).

The declining representation of rice rats in later horticultural deposits might indicate that the "vermin" problem either was under control or had declined in the face of considerable pressure both from humans and their dogs. Ultimately, habitat destruction and the introduction of predators/competitors such as cats, mongoose, and Old World rats during the post-Columbian era drove rice rats to extinction.

Such a pattern would imply a relationship between gardening, food storage, predation, and the numbers of rice rats in archaeological deposits that has little to do with preference for or prejudice against marine resources. It is important, however, to emphasize that without a better pre-Saladoid, Saladoid, and post-Saladoid stratigraphic sequence, change through time in the use of rice rats on Montserrat or an association of their use with gardening cannot be proven.

CONCLUSION

An important aspect of Caribbean cultural history is the role played by terrestrial animals in Saladoid subsistence efforts as they colonized the island chain. The data from Trants indicate that people living there used both terrestrial and marine resources. Use of indigenous terrestrial fauna and transportation of exotic animals throughout the island system were important characteristics of colonization in the Lesser Antilles. Perhaps some terrestrial resources could not support the combination of long-term exploitation and predation by introduced carnivores and eventually became extinct, leaving only their skeletal remains to remind us of their existence.

On a regional scale, Trants provides additional evidence that extensive use of terrestrial resources was a consistent Saladoid feature, but that there was much variation among Saladoid occupations in the Lesser Antilles. Many different subsistence strategies were practiced in the Lesser Antilles by Saladoid peoples, each one reflecting local conditions. Future work in the Caribbean should attempt to explore temporal variation and activity areas within Saladoid settlements such as Trants.

ACKNOWLEDGMENTS

I would like to thank David R. Watters and James B. Petersen for the opportunity to study the Trants collection. I appreciate the assistance of Joel A. Dukes with the identifications and permission from Elizabeth S. Wing to use the comparative collection at the Florida Museum of Natural History. I am also grateful to Elizabeth Wing and Anne Stokes for access to their manuscripts while in unpublished form. Funding was provided by the Carnegie Museum of Natural History, the University of Maine at Farmington, and the Charles Cohn Foundation. Earlier versions of this paper were presented at the 58th Annual Meeting of the Society for American Archaeology in St. Louis, Missouri, and at the 15th International Congress for Caribbean Archaeology, San Juan, Puerto Rico.

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A NEW SPECIES OF *ANTOCHA* (SUBGENUS *ORIMARGULA*)
FROM SULAWESI (DIPTERA: TIPULIDAE) AND
ITS MATE-CLASPING BEHAVIOR

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ABSTRACT

Antocha (*Orimargula*) *possessiva* n. sp., the first species in the subgenus *Orimargula* from Sulawesi, and its unusual behavior involving precopulatory mate-clasping are described. Males clasp females from below over the pleural region of the fifth abdominal segment, and then ride on them dorsally. Expansion and folding of the pleural region of the fifth abdominal segment of females, and enlarged basistyles of males, facilitate nongenital coupling, and are hypothesized as resulting from sexual selection favoring precopulatory mate clasping.

INTRODUCTION

The genus *Antocha* Osten Sacken (1860) is a cosmopolitan genus of small-sized crane flies within the tribe Limoniini (Tipulidae: Limoniinae). The genus is characterized by a prominent anal angle on the wing. Three subgenera are recognized: *Antocha* Osten Sacken (1860), *Orimargula* Mik (1883), and *Proantocha* Alexander (1919). The subgenus *Orimargula* can be separated morphologically from the other two subgenera of *Antocha* by wing venation that lacks a discal cell (Mik, 1883). *Antocha* (*Orimargula*) is an Old World group, represented by 21 species in the Ethiopian region, three in the Australasian region, three in the Palearctic region, and 15 in the Oriental region. In Southeast Asia, species of this subgenus have been recorded only from Borneo and Sumatra. In 1985 an undescribed species of *Antocha* (*Orimargula*) was collected on Sulawesi, the first record of the subgenus from that island. This new species and its unusual mate-clasping behavior are described in this paper.

SYSTEMATICS

Antocha (*Orimargula*) *possessiva* Young, new species

(Fig. 1-5)

Diagnosis.—This Indomalayan species of Limoniini is placed in the subgenus *Orimargula* because the wing venation lacks a discal cell (Fig. 1). It differs from all other described species of *Orimargula* by features of the male genitalia, especially the elongated basistyles (Fig. 3), and the modification of the pleural region of the fifth abdominal segment of females (Fig. 5).

Description.—Morphological terminology follows Byers (1961) and Young (1987). Description is based on seven males and four females preserved in 80% ethanol. Body length: male, 4.0–4.5 mm; female, 4.5–5.0 mm. Wing length: male, 4.0 mm; female, 4.5 mm.

Head: Occiput brown, with black setae. Rostrum pale yellow. Eyes large, separated at vertex by about two-thirds width of eye in frontal view, narrowly separated ventrally by width of two rows of ommatidia. Antenna 16-segmented, filiform; scape cylindrical, two times as long as wide; pedicel

Submitted 8 April 1994.

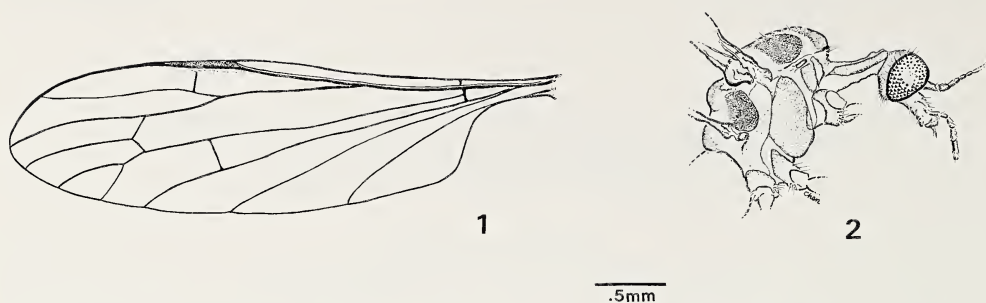


Fig. 1-2.—*Antocha (Orimargula) possessiva*. 1, wing; 2, head and thorax, right lateral view.

globular; flagellomeres subcylindrical, verticillate; basal flagellomeres distinctly elongated; apical flagellomere 1.5 times as long as penultimate.

Thorax: Grayish brown to dark brown, with velvety-black patches. Cervical sclerites greatly elongated, attached to thorax ventrally (Fig. 2). Pronotum extremely reduced, with setae near anterior margin. Prescutum enlarged and projecting anteriorly, dark brown anteromedially, fading to grayish brown at midlength; lateral border of prescutum with a large velvety-black patch. Scutum, scutellum, and postnotum brown. Pleura grayish brown; anepisternum and pre-episternum dark brown; laterotergite with large velvety-black patch. Legs yellowish brown; claws dark brown, each claw with single tooth at basal third. Wings (Fig. 1) subhyaline, faintly tinged with grey; stigma indistinct; R_s long, gently convex, slightly shorter than R_3 ; R_2 and R_{2+3} subequal. Halteres pale brown.

Abdomen: Pale brown. Pleural region modified on fifth segment of females (Fig. 5). Fifth tergum with lateral area greatly expanded (especially anterolateral corners), which overlap pleural regions; pleural membrane compressed, forming narrow thickened band, invaginated at basal third. Posterolateral corners of terga with 10–16 setae; posterolateral edge of fifth tergum below setae expanded ventrolaterally into pleural region.

Male Genitalia: Hypopygium as in Fig. 3. Ninth tergum narrow, posterior margin straight. Basistyle relatively long, slender; ratio of length of ninth tergum to length of basistyle is 0.3. Ninth sternum simple, undivided, rounded at posterior apex. Dististyles elongate, fused basally for two-thirds of length. Dorsal dististyle glabrous, subarcuate, acute apically. Ventral dististyle simple, setiferous, deflected medially at right angle to basistyle; apex recurved anteromedially. Lateral process simple,

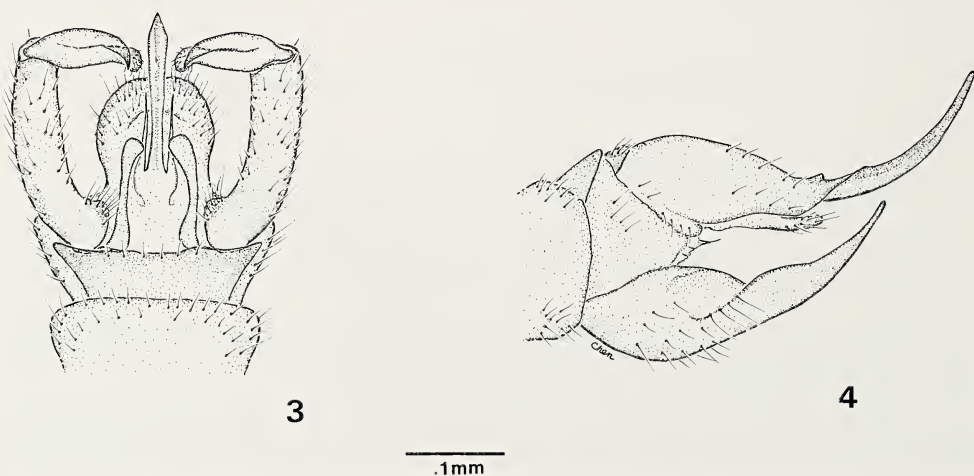


Fig. 3-4.—*Antocha (Orimargula) possessiva*. 3, male hypopygium, dorsal view; 4, female ovipositor, lateral view.

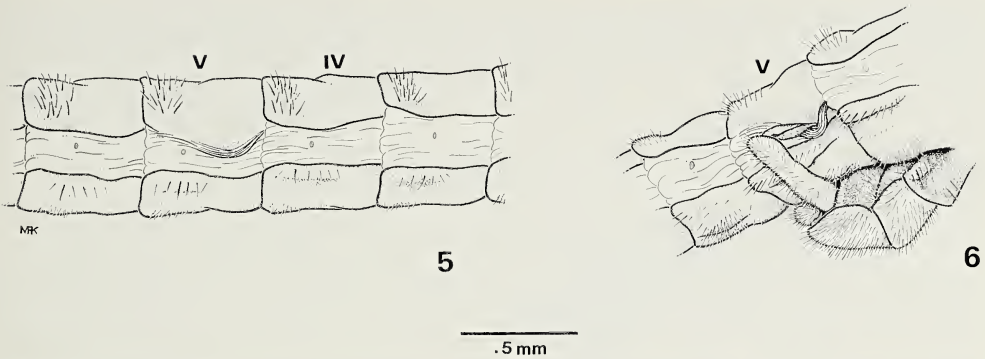


Fig. 5-6.—*Antocha (Orimargula) possessiva*. 5, female abdominal segments III-VI, right lateral view; 6, female abdomen showing male basistyles and dististyle grasping lateral part of fifth abdominal segment, ventrolateral view.

extending to near midlength of basistyle, apex slightly expanded. Aedeagal sheath well-developed, curved ventrally. Aedeagal process slender, apically acute, reaching to near midlength of aedeagal sheath.

Ovipositor (Fig. 4): Eighth tergum reduced. Ninth tergum much reduced, well-separated from tenth tergum. Cerci slightly shorter than tenth tergum, curved dorsally; dorsal surface flat, broader at base, narrowed to apex. Eighth sternum expanded laterally, wider than seventh sternum. Tenth sternum with setae near posterior margin. Hypovalues broad basally, tapered distally, extending to one-third length of cerci.

Type Material.—Holotype: male, Carnegie Museum of Natural History (CMNH). Verbatim text of three pin labels: INDONESIA: Sulawesi Utara. Dumoga-Bone N. P. 22 Aug 1985. Coll. Chen Young / Base Camp 211 m. PROJECT WALLACE / HOLOTYPE *Antocha (Orimargula) possessiva* Young [red paper]. Paratypes with same data as holotype: ten males, ten females. All specimens were collected at light. Six pair of paratypes are mounted in clasping position as retained at death. Two paratypes (one male, one female) are deposited in the collections of the National Biological Institute, Bogor, Indonesia; other paratypes deposited in CMNH.

Other Material.—Eighteen specimens (ten males, eight females) with same data as holotype preserved in 80% ethanol and deposited in CMNH.

Etymology.—The name of this species is the Latin adjective *possessivus* (-a, -um), meaning to possess, and refers to the clasping and holding of females by males.

Habitat.—Specimens of *A. possessiva* were collected at a rain forest site within the Dumoga-Bone National Park on the northern peninsula of Sulawesi. The National Park is located just north of the equator (0°38'N, 124°06'E). The site is at the eastern end of the park, on the west bank of the Tumpah River, a tributary of the Toraut River. The vegetation is primary lowland forest at approximately 200 m elevation. Specimens were collected at a white cloth sheet illuminated by a mercury vapor lamp near the edge of a pond along the Tumpah River. The pond was surrounded by rice fields with irrigation channels on three sides, and by lowland forest on one side. The river, the pond, and the larger irrigation channels are suitable and likely habitats for the immature stages of species of *Antocha*.

Remarks.—The general appearance of *A. possessiva* is similar to that of *A. praescutalis* Alexander from Moeara Tenam, southern Sumatra, and to *A. ma-*



Fig. 7.—*Antocha (Orimargula) possessiva*. Nongenital coupling of the adult, right lateral view.

culipleura Edwards from Mount Kinabalu, northern Borneo. All three species have similar velvety-black spots on the thoracic pleura. *Antocha possessiva* differs from *A. maculipleura* mainly by its smaller size and indistinct stigma. It differs from *A. praescutalis* by the absence of a third velvety-black spot on the anepisternum.

Antocha (Orimargula) possessiva is very distinct from all other species of the subgenus. Two unique characters occur in male genitalia of this species. The

basistyles are unusually long and the dorsal and ventral dististyles are almost completely fused (Fig. 3). Both features enhance the structural integrity of the male genitalia, and may increase the firmness with which the female abdomen is clasped (Fig. 6) as described below.

MATE-CLASPING BEHAVIOR (Fig. 6–7)

Unusual mate-clasping behavior was observed in this species at an illuminated cloth sheet on a clear night between 2000–2300 hr. Neither sex was observed to congregate on the sheet, and 20 males and 18 females were collected on the sheet. All flies arrived at the sheet separately and made initial contact with each other while fluttering or walking about on its surface. When a male contacted a female, he would mount her dorsally on the thorax between the wings, their bodies oriented in the same direction (Fig. 7). The male would bend his abdomen ventrally alongside the female's abdomen, and then curl it dorsally so as to clasp the pleural region of the fifth abdominal segment of the female from the ventral side (Fig. 6). This behavior was observed in nine pairs, with the position of the male's abdomen occurring (apparently randomly) on either side of the female.

After a male clasped a female, the male remained mounted on the female and tenaciously retained possession of her through firm nongenital contact. Coupled pairs were unable to fly, and if disturbed would drop to the ground or crawl across the surface of the sheet. The male's grasp was firm, and union with females persisted even after a pair was killed in cyanide, or dropped into 80% ethanol. Coupled pairs were easily mounted in conjoined position.

Male-male contact was also observed on the brightly-lit sheet. Such contact would result in brief coupling attempts by both males, and would quickly end with one or both males dislodging the other. In a few cases a solitary male contacted a male that was already clasping a female. The rival male would attempt to dislodge the guarding male and to gain access to the fifth abdominal segment of the female. Rival males were never observed to attempt genitalic copulation with the female.

Actual copulation in this species was not observed, either on the sheet or on the ground. Copulation was observed at the same time in other crane flies (species of *Nephrotoma* and *Trentepohlia*). These species assumed an end-to-end position in copula on the sheet.

DISCUSSION

The riding of females by males has not been observed previously in the genus *Antocha*, nor has it been reported in other species of crane flies. It is difficult to assess the significance of this behavior because of the artificial conditions of light and substrate at the time of observation. Several facts needed to interpret the nature of this behavior remain unknown, including the time when copulation occurs, the oviposition site, the influence of clasping on mating success of competitive males, and details of the life history. However, the presence of a pleural modification of the fifth abdominal segment of females to maintain the secure grip of elongate male basistyles suggests mutually compatible evolutionary novelties in both sexes that may have resulted from sexual selection. The persistent clasp of the females by males possibly constitutes mate-guarding behavior. Such guarding behavior can occur either before (precopulatory) or after (postcopulatory) copulation and insemination, and both conditions have been reported for other species of insects.

Precopulatory mate-guarding has been described in the hippoboscid fly, *Lynchia hirsuta* (Thornhill and Alcock, 1983). Females of this species lay eggs individually over a considerable period of time. Males can identify females that are about to become receptive to mating, and females mate more than once at intervals throughout their lives. These factors favor selection of precopulatory female-riding by males because such behavior increases the likelihood that the sperm of the riding male will fertilize the eggs as they are produced and laid over time.

In *A. possessiva* and tipulid species in general, adult longevity is relatively short. Females generally carry a full complement of mature eggs at emergence and mate at or very soon after emergence (Pritchard, 1983); females usually lay eggs rapidly over a relatively short period of time. These conditions decrease the time over which reproductive advantage might be gained by males via precopulatory riding. In addition, because females in two out of the six coupled pairs of *A. possessiva* observed in this study were without eggs, it is assumed that males of this species are unable to determine the gravid condition in females, or are indifferent to it. Neither of these circumstances favor selection for male behavior involving precopulatory riding.

Postcopulatory mate-guarding behavior was first reported in three species of Limoniinae by Adler and Adler (1991). The three species involved are *Antocha saxicola* Osten Sacken, *Dactylolabis montana* (Osten Sacken), and *Limonia simulans* (Walker). Adler and Adler observed the males of these species guarding their mates at oviposition sites after uncoupling. They concluded that all three species were polygamous and sex ratios at oviposition sites were male-biased. Sperm competition appears to be intense and to favor the last male to mate.

The sex ratio of *A. possessiva* at the sheet was not male-biased, although the sex ratio at natural oviposition sites remains unknown. It is possible that the observed sex ratios and behavior observed here are artifacts of unnatural encounters at the mercury lamp, and reflect behavior normally associated with postcopulatory coupling at oviposition sites nearby. This would explain the tenacity of the coupling, and the apparent indifference of males to gravid and nongravid females. However, abdominal clasping of females by males, and not copulation, was observed between male and female flies during their initial encounters at the sheet. In addition, rival males appear to compete for possession of the fifth abdominal segment of females, rather than for direct genitalic contact. Neither of these factors supports the hypothesis that clasping behavior is postcopulatory. In fact, postcopulatory guarding of a female that has been previously mated by another male would not increase reproductive fitness of the guarding male. For the above reasons, in addition to those presented by Thornhill and Alcock (1983) in *Lynchia*, the observed behavior of *A. possessiva* is interpreted as precopulatory mate guarding.

Pritchard (1983) indicated that some Limoniinae display true mating swarms. I observed a swarm of *Antocha saxicola* (Pennsylvania, Monroe County, Pocono Lake Reservoir, 20 May 1985) and captured both males and females from it. It is possible that *A. possessiva* also forms swarms in which males and females make contact and form riding pairs. The absence of sexual dimorphism in the antennae suggests that pheromones are probably not involved in this species (Pritchard, 1983). If mating occurs within such swarms in *A. possessiva*, then coupled pairs might drop from the mating swarm and crawl to a suitable oviposition site where copulation would take place. Because riding by the male on the female prevents the female from flying, the mating swarm would most likely occur very close to

or directly over the habitat where oviposition occurs and where the immature stages develop.

It is also possible that precopulatory contact between males and females is mandatory in order to stimulate females in the right microhabitat to permit copulation or to release oviposition. Aspects of female choice may be involved, although variation in male reproductive success was not observed in this study. Alternative interpretations are also possible with male-clasping inhibiting females from mating, or with males being required at oviposition sites in order to mechanically assist with oviposition. *Antocha* is one of the very few genera of crane flies in which the larvae have lost all functional spiracles and are truly aquatic in habit (Byers, 1978). The immature stages and life cycle of only one *Antocha* species, *A. saxicola*, has been studied (Alexander, 1919; Fuller and Hynes, 1987).

In summary, the female-riding behavior observed in this study is hypothesized as precopulatory mate-guarding behavior. Because this unusual behavior was observed under artificial conditions at a collecting light and sheet, the specific nature of the behavior as presented above is speculative. Further observations on life history are needed, especially of mating behavior and oviposition under natural conditions. Of particular value will be observations that will determine the timing and occurrence of copulation in relation to precopulatory clasping.

ACKNOWLEDGMENTS

This paper is Project Wallace Paper No. 143, and is based on material collected by the author on Project Wallace, sponsored by the Indonesian Institute of Sciences and the Royal Entomological Society of London. The research was supported by a grant from the M. Graham Netting Field Research Fund, The Carnegie Museum of Natural History, Pittsburgh. I would like to thank J. E. Rawlins for comments and suggestions on the manuscript, R. L. Davidson for literature translation, M. A. Klingler for preparing Fig. 5–7, Mary Ann Daman for manuscript preparation, and three anonymous reviewers for their comments on the manuscript.

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A REVISED CLASSIFICATION OF THE
SPIRIFERID BRACHIOPODS

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ABSTRACT

A new classification of the impunctate and punctate spiriferid brachiopods is presented. Where morphological evidence permits, ancestor-descendant relationships are discussed and indicated.

New taxa include the suborder Cyrtinidina Carter and Johnson; new families are Ulbospiriferidae Johnson and Carter, Lazutkinidae Johnson and Hou, Elymospiriferidae Johnson and Hou, Tenellodermidae Carter, Johnson, and Gourvennec, Perissothyrididae Carter, Palaeochoristitidae Carter, Skelidorygmidae Carter, Rastelligeridae Carter, Dimegelasmidae Carter, Spiropunctiferidae Carter; new subfamilies are Callispiriferinae Johnson, Eureka spiriferinae Johnson, Branikiinae Johnson and Hou, Ulbospiriferinae Johnson and Carter, Palaeospiriferinae Carter, Johnson, and Hou, Howellellinae Johnson and Hou, Araspiriferinae Johnson, Eomartiniopsinae Carter, Elivellinae Carter, Sergospiriferinae Carter, Tangshanellinae Carter, Reticulariopsinae Gourvennec, Rhenothyridinae Gourvennec, Obesariinae Gourvennec, Eoreticulariinae Gourvennec, Quadrithyridinae Gourvennec, Martinothyridinae Carter, Tornyiferinae Carter, Spinolepismatininae Carter, Paralepismatininae Carter, Rastelligerinae Carter, Dentospiriferinae Carter, Yalongiinae Carter, Pseudocyrtininae Carter, Dispiriferinae Carter, Tethyspirinae Carter, Paralaballinae Carter, and Jiangdospiriferinae Carter.

INTRODUCTION

In 1985 the organizers of the First International Congress on Brachiopods (Brest) sponsored a revision of the out-of-date brachiopod Treatise volumes. We were given the task of revising the spiriferids, impunctate and punctate. In the absence of any recent comprehensive revision and classification for this large group we submit the following preliminary classification of the spiriferid brachiopods for the examination and criticism of our colleagues. We recognize that no endeavor of this magnitude can be perfect or complete and beg the indulgence of our colleagues for any egregious errors or omissions. Now is the time to bring errors or omissions to our attention, before the Treatise goes to the press.

Since the first publication of the brachiopod volumes of the Treatise on Invertebrate Paleontology (Williams et al., 1965) a great deal of new information about spiriferid brachiopods has accrued concerning their diversity, morphology,

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distribution, and phylogenetic relationships. This is especially true for the spiriferid brachiopods. For example, in the first edition of the Treatise Pitrat (1965) recognized 187 spiriferid genera. Over 340 additional genera have been described in the intervening years, almost tripling the number of genus-level taxa. Also, numerous family-level taxon proposals have accompanied this descriptive explosion, often without discussion or written justification for the new taxa. Thus, a new evaluation of genera and their assignment to higher taxa is clearly in order.

Waterhouse (1968), Ivanova (1972), and Carter (1974) offered revised classifications for part or all of the spiriferid brachiopods soon after publication of the original Treatise volumes. These classifications are long outdated and have been emended numerous times or ignored. None has been accepted as a standard for the group.

In the following classification considerable emphasis is placed on shell structure (orders), growth form (suborders or superfamilies), internal structures (families or subfamilies), and micro-ornament (all family levels). Several possible synapomorphies are identified: taleola-like denticles in the Spiriferoidea and Paeckelmanelloidea, biramous spines in the Elythidae, the tichorhinum in the Cyrtinidae, development of a syrinx in the Syringothyridoidea, crenulation of the hingeline in the Superfamily Spondylospiroidea.

Although cladistic analysis was not performed in constructing this classification, it is hoped that it reflects the phylogeny of the spiriferids to a large degree. Carlson (1991), in a phylogenetic study of the brachiopod superfamilies, pointed out that the spiriferids, as classified in the 1965 Treatise, were not monophyletic and did not comprise a clade. She is presently reanalyzing this group using some of the information provided here.

Order Spiriferida Waagen, 1883

[*nom. correct.* Moore, Lalicker, and Fischer, 1952, p. 221

(*pro* order Spiriferacea Kuhn, 1949, p. 104;

nom. transl. ex suborder Spiriferacea Waagen, 1883, p. 447),

emend. Carter, Johnson, Gourvennec, and Hou, herein]

Diagnosis.—Generally biconvex; generally transverse with moderately wide to extended straight hingeline; ribbing very fine to coarse; small dorsal and larger ventral interareas always developed; spiralia directed laterally or posterolaterally with primary lamellae parallel and close to sagittal plane; jugum absent; shell substance impunctate.

Discussion.—The Order Spiriferida comprises the impunctate strophic brachiopods with a spiral brachidium and ranges from the Upper Ordovician to the Upper Permian. The oldest suborder, Spiriferidina Waagen, 1883, is represented in the Lower Paleozoic by eospiriferid genera such as *Eospirifer* and *Macroleura* that bear a capillate shell fabric and a simple interior with dental and crural plates and lack a ctenophoridium. Several authors (Rudwick, 1970; Ivanova, 1972) have suggested derivation of the order from an impunctate strophic orthid based on general morphology and age of first appearance. We tend to agree with this suggestion but cannot with confidence propose a likely intermediate ancestor. Gourvennec and Mélou (1990) recently demonstrated the similarity between the micro-ornament of the Upper Ordovician orthid genus *Ptychopleurella* and that of the spiriferid genus *Hysterolites*. However, this similarity could be accounted for by convergent or parallel evolution.

Rong et al. (1994) recently described a Late Ordovician (mid-Ashgill) species of *Eospirifer* from eastern China. This primitive species lacks crural plates and has very simple posterior cardinalia, quite unlike any known orthid. Furthermore, "spiriferoid" orthids such as *Platystrophia* or *Mcewanella* are not known from any of the areas where primitive eospiriferids have been recovered. Although the brachidium is not known for these early Chinese eospiriferids the simple cardinalia are reminiscent of some early atrypids and the possibility remains that the impunctate spiriferids may have been derived from the atrypids, not the orthids. It can be seen from these discoveries that more evidence is needed to ascertain the true ancestors of the spiriferids.

The Devonian history of the Spiriferidina is one of proliferation and diversity exemplified by the superfamilies Spinelloidea and Theodossioidea, lacking a delthyrial plate, and the Cyrtospiriferoidea, which have that structure. Late in the Famennian the Theodossioidea gave rise to several genera assigned to the Ulbospiriferidae, with an inner prismatic shell layer such as is found commonly in various Carboniferous and Permian spiriferids. Late in the Devonian the theodossioids, probably an ulbospiriferid, gave rise to several superfamilies that became dominant elements of the Late Paleozoic brachiopod faunas, namely the Spiriferoidea, Paeckelmanelloidea, and Brachythyridoidea.

Soon after the proliferation of the capillate Spiriferidina the Delthyridina appeared as a second major branch of impunctate genera, including *Howellella* and *Delthyris*, and characterized by a fimbriate shell fabric. Remnants of a transitional shell fabric are present in the Silurian and Lower Devonian Cyrtinopsididae and Acrospiriferidae of the Superfamily Delthyridoidea, but by the Middle Devonian the two suborders were well represented and distinct. The Devonian history of the Delthyridina is also one of proliferation and diversity, represented by numerous families and subfamilies. By the Carboniferous most of the delthyridoid families had disappeared, but the reticularioids, which arose from the Delthyridina in the Silurian, flourished with great diversity until the end of the era.

The origin of the Delthyridina is not known. Gourvennec (1989, 1991) has amply demonstrated that the micro-ornament of this group is substantially different from that of the eospiriferids. It is possible that the Delthyridina were derived from a group other than the eospiriferids or from a common ancestor, in which case the Spiriferida, as presented here, is diphyletic.

Two additional superfamilies, the Ambocoelioidea and the Martinioidea, split off from the Spiriferidina in the Silurian. There has been uncertainty about the derivation of these two superfamilies in the past. The ambocoeliids were judged by Pitrat (1965) to have been derived from an eospiriferid ancestor, but this was disputed by Ivanova (1972) who regarded both the Ambocoelioidea and Martinioidea as having separated from the Delthyridina. Here, we follow Pitrat and also Johnson and Lenz (1992) in regarding the ambocoelioids as having originated from an eospiriferoid stock. We argue here for a similar derivation of the martinioids on the basis of shell fabric and internal morphology of early genera. Ambocoelioid genera are common and diverse in the Devonian, but were reduced to less than a dozen genera in the Late Paleozoic. The martinioids are much less diverse and sporadically represented in the Devonian, but became numerous and diversified in the Carboniferous and Permian, just before their extinction in the Late Permian.

Stratigraphic Range.—Upper Ordovician–Upper Permian.

Suborder Spiriferidina Waagen, 1883

[*nom. correct.* Pitrat, 1965, p. H668

(pro suborder Spiriferacea Waagen, 1883, p. 447)]

[*emend.* Carter, Johnson, and Gourvennec, herein]

Diagnosis.—Lateral slopes plicate or costate; fold and sulcus commonly well developed; fine ornament, if present, capillate, pustulose, or imbricate; spinose ornament absent; ctenophoridium absent in early forms.

Stratigraphic Range.—Upper Ordovician–Upper Permian.

Superfamily Cyrtioidea Frederiks, 1924

[*nom. correct.* Johnson, Gourvennec, and Hou, herein

(pro superfamily Cyrtiacea Pitrat, 1965, p. H668);

nom. transl. Pitrat, 1965, (ex Cyrtiinae Frederiks, 1924, p. 312)]

Diagnosis.—Biconvex, commonly with fold and sulcus, smooth or plicate; ornament of nonspinose capillae crossed by variably nodose growth lines; deltidium, delthyrial plate, or stegidial plates may be present; dental plates present; crural plates well developed, rudimentary, or lacking.

Stratigraphic Range.—Upper Ordovician (Middle Ashgill)–Lower Devonian (Emsian).

Family Cyrtiidae Frederiks, 1924

[*nom. transl.* Ivanova, 1959, p. 55 (ex Cyrtiinae Frederiks, 1924, p. 312)]

[=Eospiriferinae Schuchert, 1929, p. 20]

Diagnosis.—Delthyrial plate and stegidial plates lacking; crural plates commonly well developed.

Stratigraphic Range.—Upper Ordovician (Middle Ashgill)–Lower Devonian (Emsian).

Subfamily Cyrtiinae Frederiks, 1924

[Cyrtiinae Frederiks, 1924, p. 312]

Diagnosis.—Ventribiconvex, ventral valve hemipyramidal, with catacline or procline interarea, narrowly elongate delthyrium; deltidium with medial foramen; ctenophoridium absent.

Discussion.—The species *Cyrtia approximans* (Barrande, 1879) was listed as Devonian Ff2 by Barrande (1879) and from the Acanthopyge Limestone by Havlíček, (1959:75). This led Boucot (1963) to list the upper range of *Cyrtia* as lower Devonian, but other Devonian occurrences of *Cyrtia* have not been verified. A query to Havlíček brought the following response (written communication, July 11, 1991): “*Cyrtia approximans* (Barrande) is a true *Cyrtia*! The data about its age and type locality, however, are not correct in Barrande’s paper. After revising this species, I came to the conclusion that *Cyrtia approximans* is conspecific with the Silurian *Cyrtia spiriferoides* Bouček, 1941 (Wenlock, Motol Formation).”

Stratigraphic Range.—Upper Silurian (Upper Wenlockian–Ludlovian).

Genera Included.—*Cyrtia* Dalman, 1828; *Plicocyrtia* Boucot, 1863; *Dongbeipirifer* Liu, 1977.

Subfamily Eospiriferinae Schuchert, 1929

[Eospiriferinae Schuchert in Schuchert and Levene, 1929, p. 20]

Diagnosis.—Biconvex with curved, commonly apsacline ventral interarea and open delthyrium; deltidium present; ctenophoridium commonly absent.

Discussion.—In the list below of assigned genera we retain *Macropleura* although it was regarded as a junior subjective synonym of *Hedeina* after the type species of *Hedeina* was made known by Brunton et al. (1967). Boucot (1975:362) suggested retaining *Macropleura* for large-sized Lower Devonian species, but we propose to include both large and small species based on the amplitude of plications and interspaces rather than on shell size. *Macropleura* has a few prominent plications and deep, U-shaped interspaces. *Hedeina* is characterized by broad, low plications and shallow interspaces. Probably, *Hedeina* was derived from *Eospirifer* and belongs to a different branch of eospiriferid phylogeny than *Macropleura*. Our definition would include *Hedeina ananias* Johnson, Boucot, and Murphy (1976) in *Macropleura*. We also synonymize *Ejnespirifer* Fu, 1982 with *Macropleura* on the same basis. According to Rong Jia-yu (written communication, March 6, 1994) the type species of *Ejnespirifer* does not have strut-like accessory plates in the dorsal valve as were illustrated by Fu (1982:177, fig. 92B).

Stratigraphic Range.—Upper Ordovician (Middle Ashgill)—Lower Devonian (Emsian).

Genera Included.—*Eospirifer* Schuchert, 1913; *Badainjarania* Zhang, 1981; *Endospirifer* Tachibana, 1981; *Espella* Nilova, 1965 [= *Laevispirifer* Ushatinskaia, 1977]; *Havlicekia* Boucot, 1963; *Hedeina* Boucot, 1957; *Janius* Havlíček, 1957; *Lobvia* Breivel and Breivel, 1977; *Macropleura* Boucot, 1963 [= *Ejnespirifer* Fu, 1982]; *Mictospirifer* Johnson, 1995; *Myriospirifer* Havlíček, 1978 [= *Acutilineolus* Amsden, 1978]; *Nurataella* Larin, 1973 [= *Baterospirifer* Rong, Su, and Li, 1984]; *Striispirifer* Cooper and Muir-Wood, 1951; *Yingwuspirifer* Rong, Xu, and Yang, 1974; *Xinanospirifer* Rong, Xu, and Yang, 1974.

Family Hedeinopsidae Gourvennec, 1990

[*nom. transl.* Johnson, herein

(*ex Hedeinopsinae* Gourvennec, 1990, p. 142)]

Diagnosis.—Plicate, ventribiconvex, with stegidial plates and delthyrial plate; crural plates rudimentary or absent; ctenophoridium present.

Stratigraphic Range.—Upper Silurian (Wenlockian–Pridolian).

Subfamily Hedeinopsinae Gourvennec, 1990

[*Hedeinopsinae* Gourvennec, 1990, p. 142]

Diagnosis.—As for the family.

Discussion.—Examination of the holotype of *Tannuspirifer dixon* Jones (1980: pl. 1, fig. 1), on loan from Jones, reveals that it has stegidial plates.

Stratigraphic Range.—Upper Silurian (Wenlockian–Pridolian).

Genera Included.—*Hedeinopsis* Gourvennec, 1990; *Tannuspirifer* Ivanova, 1960.

Superfamily Spinelloidea Johnson, 1970

[*nom. transl.* Johnson and Hou, herein

(*ex Spinnellinae* Johnson, 1970, p. 205)]

Diagnosis.—Biconvex, with fold and sulcus; plicate; ornament nonfrilly, capillate; delthyrial plate lacking; dental plates, without median septum.

Stratigraphic Range.—Upper Silurian (Wenlockian)—Upper Devonian (Upper Famennian).

Family Spinellidae Johnson, 1970

[*nom. transl.* Wang and Rong, 1986, p. 200

(*ex Spinellinae* Johnson, 1970, p. 205)]

Diagnosis. — Multiplicate, with smooth or medially grooved fold and smooth or medially plicate sulcus.

Stratigraphic Range. — Upper Silurian (Wenlockian)–Upper Devonian (Upper Famennian).

Subfamily Spinellinae Johnson, 1970

[Spinellinae Johnson, 1970, p. 205]

[=Guerichellinae Paeckelmann, 1931, p. 24]

Diagnosis. — Multiplicate, with smooth fold and sulcus, or with medial plication in sulcus; crural plates short or lacking.

Stratigraphic Range. — Lower Devonian (Pragian)–Upper Devonian (Upper Famennian).

Genera Included. — *Spinella* Talent, 1956; *Acutathea* Stainbrook, 1945; *Adolfia* Gürich, 1909 [= *Guerichella* Paeckelmann, 1913; = *Changshaispirifer* Zhao, 1977]; *Allanella* Crickmay, 1953 [= *Minutilla* Crickmay, 1967]; *Chimaerothyris* Paulus, Struve, and Wolfart, 1963; *Eospiriferina* Grabau, 1931; *Fidespirifer* Liashenko, 1973; *Guicyrtia* Wang and Zhu, 1979; *Volgospirifer* Shevchenko, 1970.

Subfamily Pinguispiriferinae Havlíček, 1971

[Pinguispiriferinae Havlíček, 1971, p. 27]

Diagnosis. — Plicate, with weak to obscure capillae, crossed by fila; crural plates short or lacking.

Discussion. — Several genera of the Pinguispiriferinae have been classified with the eospiriferids in the past, but although capillate they lack the well-developed capillae typical of eospiriferids. Others differ also in the construction of the cardinalia. *Nikiforovaena* Boucot, 1963, previously unknown in the dorsal interior, was examined by preparing a dorsal internal mold of the type species; it revealed the presence of a ctenophoridium and short, divergent crural plates.

Stratigraphic Range. — Upper Silurian (Wenlockian)–Middle Devonian (Eifelian).

Genera Included. — *Pinguispirifer* Havlíček, 1957; *Amoenospirifer* Havlíček, 1957; *Brevispirifer* Cooper, 1942; *Ljudmilispirifer* Cherkasova, 1976; *Nikiforovaena* Boucot, 1963; *Spirispirifer* Havlíček, 1971.

Subfamily Callispiriferinae Johnson, **new subfamily**

Diagnosis. — Non-capillate, with high flat ventral interarea.

Stratigraphic Range. — Lower Devonian (Emsian).

Genera Included. — *Callispirifer* Perry, 1984; *Rochtex* Havlíček, 1990.

Subfamily Eureka spiriferinae Johnson, **new subfamily**

Diagnosis. — Capillate, with dorsal adminicula.

Discussion. — The presence of dorsal adminicula in *Eureka spirifer* suggests an even greater separate ranking than subfamily, but as no closely related genera are now known proposal of a more substantial taxonomy seems inappropriate.

Stratigraphic Range. — Lower Devonian (Lower Emsian).

Genera Included. — *Eureka spirifer* Johnson, 1966.

Family Echinospiriferidae Liashenko, 1973

[Echinospiriferidae Liashenko, 1973, p. 109]

[=Rigauxidae Brice, 1988, p. 371]

Diagnosis.—Multiplicate, with plicate fold and sulcus.

Discussion.—A specimen of the type species of *Arctospirifer* Stainbrook, 1950 was sectioned confirming the absence of a delthyrial plate and the absence of crural plates. *Regauxia* Brice, 1988 includes the widely represented North American species *Spirifer orestes* Hall and Whitfield and *Spirifer strigosus* Meek, both of which have been assigned mistakenly to *Indospirifer* Grabau, 1931 by various authors.

Stratigraphic Range.—Lower Devonian (Pragian)—Upper Devonian (Upper Famennian).

Genera Included.—*Echinospirifer* Liashenko, 1973; *Adolfspirifer* Krylova, 1962; *Arctospirifer* Stainbrook, 1950; *Enchondrospirifer* Brice, 1971; *Hispidaria* Cooper and Dutro, 1982; *Howittia* Talent, 1956 [= *Glyptospirifer* Hou and Xian, 1975]; *Indospirifer* Grabau, 1931 [= *Schizospirifer* Grabau, 1931]; *Regauxia* Brice, 1988; *Sergunkovia* Nalivkin, 1979.

Superfamily Theodossioidea Ivanova, 1959

[*nom. transl.* Johnson, Carter, and Hou, herein

(*ex* Theodossiinae Ivanova, 1959, p. 61)]

Diagnosis.—Uniformly plicate or costate, with fold and sulcus indistinct or lacking; delthyrial plate lacking.

Discussion.—The superfamily Theodossioidea, with its one new family and three new subfamilies, unites genera that are plicate or costate over the entire exterior and which lack a well-defined fold and sulcus. An implication in this classification is that there are genetic links from the earliest genera of the subfamily Branikiinae, of Emsian age, to the Middle Devonian genera of the Theodossiinae. However, the origin of the Branikiinae is uncertain. The genus *Theodossia* is the supposed link to Famennian and younger genera of the Ulbospiriferidae, which are characterized by the presence of an inner prismatic shell layer. The Early and Middle Devonian genera are uncommon taxa and this together with their unusual morphology has resulted in their previously being outside of generally accepted spiriferid systematics.

Stratigraphic Range.—Lower Devonian (Pragian)—Upper Devonian (Upper Famennian).

Family Theodossiidae Ivanova, 1959

[*nom. transl.* Johnson, Carter, and Hou, herein

(*ex* Theodossiinae Ivanova, 1959, p. 61)]

Diagnosis.—Without inner prismatic shell layer.

Stratigraphic Range.—Lower Devonian (Pragian)—Upper Devonian (Frasnian).

Subfamily Theodossiinae Ivanova, 1959

(Theodossiinae Ivanova, 1959, p. 61)

Diagnosis.—Capillate.

Stratigraphic Range.—Middle Devonian (Eifelian)—Upper Devonian (Frasnian).

Genera Included.—*Theodossia* Nalivkin, 1925 [= *Vandergrachtella* Crickmay, 1953]; *Paralazutkinia* Jiang, 1978 [= *Pinghuangella* Jiang, 1978]; *Urella* Rzhonitskaia, 1960 [= *Retzispirifer* Kulkov, 1960].

Subfamily Branikiinae Johnson and Hou, **new subfamily**

Diagnosis. — Noncapillate.

Stratigraphic Range. — Lower Devonian (Pragian)–Middle Devonian (Eifelian).

Genera Included. — *Branikia* Havlíček, 1957 [= *Bidentatus* Khodalevich and Breivel, 1972]; *Jilinospirifer* Su, 1980; *Lenzia* Perry, Boucot, and Gabrielse, 1981.

Family Ulbospiriferidae Johnson and Carter, **new family**

Diagnosis. — With inner prismatic shell layer.

Stratigraphic Range. — Upper Devonian (Upper Famennian).

Subfamily Ulbospiriferinae Johnson and Carter, **new subfamily**

Diagnosis. — Uniformly costate.

Stratigraphic Range. — Upper Devonian (Upper Famennian).

Genera Included. — *Ulbospirifer* Grechishnikova, 1965; *Cyrtiorina* Cooper and Dutro, 1982; *Tenisia* Martynova, 1970 [= *Omolonospirifer* Simakov, 1970].

Subfamily Palaeospiriferinae Carter, Johnson, and Hou, **new subfamily**

Diagnosis. — With low, rounded plications.

Stratigraphic Range. — Upper Devonian (Upper Famennian).

Genera Included. — *Palaeospirifer* Martynova and Sverbilova, 1968 [= *Goungjunspirifer* Zhang, 1983].

Family Palaeochoristitidae Carter, **new family**

Diagnosis. — Cardinal extremities rounded in juveniles, outline variable in adults; well-developed dental adminicula and dorsal adminicula present; micro-ornament absent.

Discussion. — The origins of this family are obscure because dorsal adminicula are rare in the Theodossioidea. The only known Devonian theodossioid genus with dorsal adminicula is the Russian Middle Devonian genus *Urella* Rzhon-snitskaya, 1960, which is presumed to be in the line of ancestry of the palaeochoristitids.

Stratigraphic Range. — Lower Carboniferous (Tournaisian).

Genera Included. — *Palaeochoristites* Sokolskaya, 1941; *Eochoristites* Chu, 1933 [= *Centrospirifer* Tien, 1938].

Superfamily Cyrtospiriferoidea Termier and Termier, 1949

[*nom. transl.* Ivanova, 1972, p. 31

(*ex* Cyrtospiriferinae Termier and Termier, 1949, p. 99)]

Diagnosis. — Nonfrilly, capillate or pustulose; delthyrial plate present; ctenophoridium without crural plates.

Stratigraphic Range. — Lower Devonian (Emsian)–Upper Devonian (Upper Famennian).

Family Spinocyrtiidae Ivanova, 1959

[*nom. transl.* Pitrat, 1965, p. H688

(*ex* Spinocyrtinae Struve, 1963, p. 462,

nom. correct. pro Spinocyrtinae Ivanova, 1959, p. 59)]

Diagnosis. — Multiplicate, with smooth or medially grooved fold and smooth or medially plicate sulcus.

Stratigraphic Range. — Lower Devonian (Emsian)–Upper Devonian (Frasnian).

Genera Included. — *Acutoria* Cooper and Dutro, 1982; *Alatiformia* Struve, 1963;

Eosyringothyris Stainbrook, 1943; *Mediospirifer* Bublitchenko, 1956 [= *Carpinaria* Struve, 1982]; *Duryeella* Boucot, 1975; *Orthospirifer* Pitrat, 1975; *Platyrachella* Fenton and Fenton, 1924; *Spinocyrtia* Frederiks, 1916; *Subcuspidella* Mittmeyer, 1965 [= *Tenuicostella* Mittmeyer and Geib, 1967].

Family Cyrtospiriferidae Termier and Termier, 1949
[*nom. transl.* Beznosova, 1958, p. 17
(*ex* Cyrtospiriferinae Termier and Termier, 1949, p. 99)]

Diagnosis.—Nonfrilly, flanks costate; fold and sulcus finely costate.

Discussion.—The assignments of at least 19 genera to one of two subfamilies on the basis of shell shape is inadequate. A re-evaluation of the genera of the Family Cyrtospiriferidae on the basis of internal structures is obviously needed. An initial appraisal might usefully involve a determination of dental plates (intrasinal or extrasinal).

Stratigraphic Range.—Middle Devonian (Upper Givetian)—Upper Devonian (Upper Famennian).

Subfamily Cyrtospiriferinae Termier and Termier, 1949
[Cyrtospiriferinae Termier and Termier, 1949, p. 99]
[=Hunanospiriferinae Beznosova, 1958, p. 17]

Diagnosis.—Wide interarea with acute cardinal angles.

Stratigraphic Range.—Upper Devonian (Frasnian—Upper Famennian).

Genera Included.—*Cyrtospirifer* Nalivkin in Frederiks, 1924 [= *Hunanospirifer* Tien, 1938; *Grabauispirifer* Gatinaud, 1949; *Eurytatospirifer* Gatinaud, 1949; *Deothossia* Gatinaud, 1949; *Lamarckispirifer* Gatinaud, 1949; *Subquadriangulispirifer* Sartenaer, 1982]; *Austrospirifer* Glenister, 1956; *Geminisulcispirifer* Sartenaer, 1982; *Liraspirifer* Stainbrook, 1950; *Petshorospirifer* Fotieva, 1985; *Regelia* Crickmay, 1952; *Sinospirifer* Grabau, 1931; *Sphenospira* Cooper, 1954; *Syringospira* Kindle, 1909; *Tarandrosirifer* Simakov, 1970; *Tenticosirifer* Tien, 1938 [= *Conispirifer* Liashenko, 1985].

Subfamily Cyrtiopsinae Ivanova, 1972
[Cyrtiopsinae Ivanova, 1972, p. 33]
[=?Uchtsiriferidae Liashenko, 1973, p. 87]

Diagnosis.—Narrow interarea with rounded cardinal angles.

Discussion.—*Cyrtiopsis* Grabau has been widely reported in Famennian rocks, but lack of knowledge of the *Cyrtiopsis* interior, as well as lack of critical attention to shell form makes many citations of the genus dubious. Examples are in the influential paper by Crickmay (1952), including taxa he named *Cyrtiopsis nahanniensis* and *C. normandvillana*. We cite these two taxa because Crickmay provided drawings intended to represent the disposition of the dental plates as intrasinal and recurved distally (1952:pl. 72, fig. 12; pl. 74; fig. 4). We have examined specimens of these two species in the Crickmay collections, on loan from the Paleontological Research Institution, Ithaca, New York. Dental lamellae observed in internal molds of both species are intrasinal, but long and straight rather than being recurved distally. In this they resemble a prepared internal mold in our possession of the type species *C. davidsoni*, but they differ from it in shell form. *Cyrtiopsis davidsoni* has a deep, wide, and sharply bounded ventral sulcus that gives it a distinctive shell shape. We know of no North American species like it.

Stratigraphic Range.—Middle Devonian (Upper Givetian)–Upper Devonian (Famennian).

Genera Included.—*Cyrtiopsis* Grabau, 1923 [= *Grabauicyrtiopsis* Gatinaud, 1949; *Sinocyrtiopsis* Gatinaud, 1949]; *Dichospirifer* Brice, 1971; *Dmitria* Sidiachenko, 1961; *Eodmitria* Brice, 1982; *Platyspirifer* Grabau, 1931; *Uchtospirifer* Liashenko, 1957 [= *Timanospirifer*, *Nordspirifer*, and *Clivospirifer* Liashenko, 1973]; *Mennespirifer* Liashenko, 1973 [= *Komispirifer* Liashenko, 1973]; *Acutella* Liashenko, 1973.

Superfamily Ambocoelioidea George, 1931

[*nom. transl.* Johnson and Carter, herein
(ex Ambocoeliinae George, 1931, p. 42)]

Diagnosis.—Commonly small, lacking well-developed fold and sulcus; cardinal process commonly simple, knoblike; outer hinge plates broad, well developed; cruralium variably developed.

Stratigraphic Range.—Upper Silurian (Upper Wenlockian)–Permian.

Family Ambocoeliidae George, 1931

[*nom. transl.* Ivanova, 1959, p. 56
(ex Ambocoeliinae George, 1931, p. 42)]

Diagnosis.—Ventricibiconvex, smooth shells, rarely pauciplicate; commonly lacking dental plates.

Stratigraphic Range.—Upper Silurian (Upper Wenlockian)–Permian.

Subfamily Ambocoeliinae George, 1931

[Ambocoeliinae George, 1931, p. 42]

Diagnosis.—Crural plates vestigial or lacking; commonly with fine concentric growth lamellae, and fine capillae on older genera; dental plates lacking in younger genera.

Discussion.—Pitrat (1965:H667) suggested that the ambocoeliid brachiopods were derived from the Eospiriferinae, based on age of appearance, nonstriate site of dorsal diductor attachment, crural plates, and permissive similarities of fine ornament. Although Pitrat erred in attributing crural plates to the earliest ambocoeliids, the derivation seems plausible, beginning with the oldest ambocoeliid *Eoplicoplasia* Johnson and Lenz, 1992. *Eoplicoplasia* morphology suggests derivation from a plicate eospiriferid genus such as *Macroleura* Boucot. This is based on the presence of *Macroleura* in older Silurian beds (Boucot, 1963:706; Havlíček, 1980:11), similar overall shell shape, nonstriate site of dorsal diductor attachment, dental plates, and the presence on *Eoplicoplasia* of a relict eospiriferid radial ornament of fine capillae (Lenz, 1972:pl. 2, fig. 2, 21). *Eoplicoplasia* and *Plicoplasia* both lack crural plates, consistent with their assignment to the Subfamily Ambocoeliinae (Johnson and Trojan, 1982:128–129).

Stratigraphic Range.—Upper Silurian (Upper Wenlockian)–Permian.

Genera Included.—*Ambocoelia* Hall, 1860; *Attenuatella* Stehli, 1954; *Aviformia* Xian, 1988; *Biconvexiella* Waterhouse, 1983; *Bisinocoelia* Havlíček, 1953; *Cruricella* Grant, 1976; *Crurithyris* George, 1931; *Cyrtinoides* Iudina and Rzhonsnitskaia, 1985 [= *Mucroclipeus* Goldman and Mitchell, 1990]; *Dicoelospirifer* Zhang, 1989; *Echinocoelia* Cooper and Williams, 1935 [= *Pyramina* Liashenko, 1969]; *Eoplicoplasia* Johnson and Lenz, 1992; *Guangxispirifer* Xian, 1983; *Orbicoelia* Waterhouse and Piyasin, 1970; *Paracrurithyris* Liao, 1979; *Plicoplasia* Boucot,

1959; *Metaplasia* Hall and Clarke, 1893; *Spinoplasia* Boucot, 1959; *Swaicoelia* Hamada, 1968.

Subfamily Rhynchospiriferinae Paulus, 1957

[Rhynchospiriferinae Paulus, 1957, p. 51]

[=Ilmeniinae Dürkoop, 1970, p. 195]

Diagnosis.—Crural plates well developed, either discrete or joined to form a cruralium; commonly with fine capillae; dental plates present or absent.

Stratigraphic Range.—Lower Devonian (Emsian)—Upper Devonian (Frasnian).

Genera Included.—*Amboglossa* Wang and Zhu, 1979; *Ambothyris* George, 1931; *Changtangella* Xian, 1982; *Choperella* Liashenko, 1969; *Crurispina* Goldman and Mitchell, 1990; *Diazoma* Dürkoop, 1970 [= *Kelusia* Mamedov, 1978]; *Emanuella* Grabau, 1923; [= *Paraemanuella* Yang, 1977]; *Ilmenia* Nalivkin, 1941; *Ilmeniopsis* Xian, 1982; *Ilmenispina* Havlíček, 1959; *Ilmospirifer* Liashenko, 1969; *Ladjia* Veevers, 1959; *Levibiseptum* Xian, 1975; *Moravilla* Havlíček, 1953; *Rhynchospirifer* Paulus, 1957 [= *Kosirium* Ficner and Havlíček, 1975; *Biarella* Markovski, 1988]; *Zhonghuacoelia* Chen, 1978.

Family Verneuiliidae Schuchert, 1929

[*nom. transl.* Brunton, 1984, p. 101

(ex Verneuiliinae Schuchert, 1929, p. 21)]

Diagnosis.—Transverse to subcircular, biconvex, with opposite folding forming ligate to metacarinat anterior margins; ventral interarea narrow to full width of valves, with open delthyrium or restricted by apical deltidium; growth lines without capillae.

Stratigraphic Range.—Middle Devonian (Eifelian)—Lower Carboniferous.

Genera Included.—*Verneuilia* Hall and Clarke, 1893; *Minythyra* Brunton, 1984; *Nuguschella* Tiazheva, 1960.

Family Lazutkiniidae Johnson and Hou, **new family**

Diagnosis.—Wholly plicate, lacking capillae; with dental plates.

Stratigraphic Range.—Lower Devonian (Emsian)—Middle Devonian (Givetian).

Genera Included.—*Lazutkinia* Rzhonsnitskaia, 1952 [= *Yavorskiella* Lazutkin in Yavorsky, 1940]; *Prolazutkinia* Hou and Xian, 1983.

Family Eudoxinidae Nalivkin, 1979

[*nom. correct. et transl.* Carter, herein

(*pro* Subfamily Eudoxininae Nalivkin, 1979, p. 145)]

Diagnosis.—Small to very large; biconvex; costate or costellate; micro-ornament papillose in some, absent or unknown in most genera; dental adminicula and protuberant ctenophoridium absent.

Discussion.—The lack of a convex ctenophoridium in this group convincingly points to its derivation from the eospiriferid–ambocoeliid lineage. There is a great difference in size between the Early Carboniferous *Eudoxina* and *Paulonia* and the Permian *Costicrura* and *Wilberrya*. In the absence of intermediate forms of Visean or Upper Carboniferous age the homogeneity of this group cannot be tested easily.

Stratigraphic Range.—Upper Devonian (Famennian)—Upper Permian.

Genera Included.—*Eudoxina* Frederiks and Kruglov, 1928; *Costicrura* Hoover, 1981; *Paulonia* Nalivkin, 1925; *Wilberrya* Yancey, 1978.

Superfamily Martinioidea Waagen, 1883

[*nom. correct.* Carter, Johnson, and Gourvennec, herein

(*pro* Martiniacea Waagen, 1883;

nom. transl. Ivanova, 1972, p. 41,

ex Subfamily Martiniinae Waagen, 1883, p. 524)]

Diagnosis.—Biconvex, with broadly rounded lateral extremities and short hingeline; lateral slopes smooth or with subdued ribbing; micro-ornament commonly capillate, smooth, or very finely spinulose, but not strongly lamellose or concentrically disposed; ventral median septum absent; dorsal interior with ctenophoridium in all but the earliest genera, commonly with crural plates or dorsal adminicula; surface commonly pitted.

Discussion.—This superfamily is now believed to have been derived from the ambocoeliids in Late Silurian time through the acquisition of consistently inflated dorsal valves and pitted micro-ornament. The earliest family, the Tenellodermidae, lack a ctenophoridium, attesting to their derivation from the ambocoelioids. Internally, the appearance of crural plates or strong dorsal adminicula is manifested in several lineages throughout most of the history of the superfamily.

Stratigraphic Range.—Silurian (Upper Wenlock)–Upper Permian.

Family Tenellodermidae Carter, Johnson, and Gourvennec, **new family**

Diagnosis.—Ctenophoridium absent; surface pitted or simple; dental plates present.

Discussion.—In the absence of a ctenophoridium these two genera provide a convincing transition from the ambocoelioids to ctenophoridium-bearing Late Paleozoic martinoids. The earliest species of both genera occur in the Upper Wenlockian of Bohemia, but we suggest that *Tenellodermis* most closely resembles an ambocoeliid ancestor in its simple cardinalia having neither striate cardinal process nor crural plates.

Stratigraphic Range.—Silurian (Upper Wenlockian)–Middle Devonian (Eifelian).

Genera Included.—*Cingulodermis* Havlíček, 1971; *Tenellodermis* Havlíček, 1971.

Family Elythyridae Gourvennec, **new family**

Diagnosis.—Flanks plicate; ornament of fine pits or spines and pits; ctenophoridium, dental plates, and crural plates or dorsal adminicula present.

Discussion.—These genera are unified by their similar internal morphology and represent the earliest martinoids with a ctenophoridium. Externally, they vary in their micro-ornament.

Elythyna has fine elongate pits or grooves arranged in quincunx similar to the Ingelarellidae. Examination of topotype material of the type species, *E. salarica*, shows that there are short subparallel crural plates (or dorsal adminicula?) and a ctenophoridium. *Najadospirifer* Havlíček possesses discontinuous capillae with fine ovate pits radially arranged in the interspaces (Havlíček, 1971:pl. 1, 2) and internally the crural plates are very short (Boucot, 1962:pl. 49). *Tatjanaspirifer* is assigned here despite its ornament of radial marginal spinules of the reticularioid type. This genus also shows randomly distributed pits which were originally

diagnosed as coarse spine bases by Cherkessova. This pitted ornament is unknown in the reticularioids and strongly suggests affinity with the martinioids. These pits are sometimes best seen in the fibrous layer and may not be apparent unless the outer layer is exfoliated, a feature common in the martinioids.

Stratigraphic Range.—Lower Devonian (Pragian)—Middle Devonian (Givetian).

Genera Included.—*Elythyna* Rzhonsnitskaya, 1952; *Najadospirifer* Havlíček, 1957; *Tatjanaspirifer* Cherkessova, 1991.

Family Martiniidae Waagen, 1883

[*nom. transl.* Ivanova, 1959, p. 56,

ex Subfamily Martiniinae Waagen, 1883, p. 524]

Diagnosis.—Ctenophoridium present; subequally biconvex; lateral slopes smooth or weakly plicate; crural plates or dorsal adminicula absent; micro-ornament of scattered surficial pits, and/or capillae, or absent.

Stratigraphic Range.—Upper Devonian (Famennian)—Upper Permian.

Subfamily Martiniinae Waagen, 1883

[Subfamily Martiniinae Waagen, 1883, p. 524]

Diagnosis.—Lacking plates or septa in either valve; micro-ornament of fine pits only.

Stratigraphic Range.—Lower Carboniferous—Upper Permian.

Genera Included.—*Martinia* McCoy, 1844 [= *Jilinmartinia* Lee and Gu, 1980; *Paramartinia* Reed, 1949; *Pseudomartinia* Leidhold, 1928]; *Beschevella* Poletaev, 1975; *Implexina* Poletaev, 1971; *Kalitvella* Lazarev and Poletaev, 1982; *Postamartinia* Want and Yang, 1993; *Spinomartinia* Waterhouse, 1968; *Tirannia* Grunt, 1977; *Weiningia* Ching and Liao, 1974 [= *Elenchus* Aleksandrov, 1973].

Subfamily Eomartiniopsinae Carter, **new subfamily**

Diagnosis.—Dental adminicula present; lateral slopes commonly weakly ribbed; micro-ornament of fine pits or absent.

Discussion.—The genus *Eomartiniopsis* Sokolskaya has been repeatedly reported in Devonian strata but we have doubts about the validity of these reports. A detailed investigation of the dorsal interiors and micro-ornament of these species is necessary to resolve this problem. The type species lacks crural plates or dorsal adminicula. If we assume that all of the species, including Devonian ones, assigned here by Sokolskaia (1941) also lack crural plates, the number of Devonian species in need of future investigation is much reduced.

Five species were assigned to this genus by Rzhonsnitskaia (1952), but she did not provide morphological evidence for her assignment. One of them, *Spirifer kirki*, undoubtedly belongs to *Warrenella*. The same might be said for *Spirifer laevis* judging from the presence of a pseudodeltidium, strong apical callosity, deep muscle scars, etc. *Spirifer maia* was probably assigned here based on external aspect, for no information is available concerning its internal structure. Apparently *S. maia* possesses a pseudodeltidium which would suggest relationship to *Warrenella*, but more information is needed to confirm this assignment. The dorsal

interiors of *Eomartiniopsis lazutkini* and *Spirifer linguifer* have never been described.

Havlicek (1959) assigned six more Devonian species and subspecies to *Eomartiniopsis*. He later (1971) restricted his concept of the genus to include only Carboniferous species and assigned his previous species to his genera *Tenellodermis* and *Cingulodermis*. However, several Devonian species cannot be assigned to these genera. Among them, *E. sellata* [*Spirifer (Martinia) inflata sellata* Paeckelmann, 1913] is assigned here, but its dorsal interior is poorly known. The ornament of *Eomartiniopsis lazutkini* and *Spirifer linguifer*, both Eifelian and mentioned above, consists of quincuncially arranged pits, an ornament unknown in *Cingulodermis*, but which evokes the Ingellarellidae. On the other hand the described ornament of *Cingulodermis* may be an artifact of preservation and incompletely known, for it is seemingly within the lineage of *Tenellodermis* (its ancestor) and *Eomartiniopsis* (its presumed descendant), both of which possess pits.

The last Devonian species assigned to *Eomartiniopsis* is *E. zeravschanica*, a *nomen nudum*, and is very poorly known. Thus, the presence of *Eomartiniopsis* in the Devonian cannot be ascertained. It has been treated as a "grab-bag" genus for smooth, poorly described reticularioids occurring in Devonian strata. Further investigation will probably show that most Devonian species of "*Eomartiniopsis*" would be better assigned to *Cingulodermis*, *Warrenella*, or similar genera.

Stratigraphic Range.—?Devonian, Lower Carboniferous–Upper Permian.

Genera Included.—*Eomartiniopsis* Sokolskaya, 1941; *Globispirifer* Tachibana, 1964; *Heteraria* Cooper and Grant, 1976; *Kisilia* Nalivkin, 1979; *Merospirifer* Reed, 1949; *Rallacosta* Cooper and Grant, 1976.

Subfamily Elivellinae Carter, **new subfamily**

Diagnosis.—Micro-ornament of capillae and fine pits; dental plates becoming progressively shorter in younger genera.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Lower Permian.

Genera Included.—*Elivella* Frederiks, 1924; *Martiniella* Grabau and Tien, 1931; *Ushkolia* Martynova and Sverbilova, 1969; *Moumina* Frederiks, 1924.

Family Martiniopsidae Kotljar and Popeko, 1967

[*nom. transl.* Carter, herein,

ex Martiniopsinae Kotljar and Popeko, 1967, p. 182]

Diagnosis.—Dental and crural plates or dorsal adminicula present; lateral slopes commonly with weak plications; micro-ornament usually weakly to strongly capillate.

Stratigraphic Range.—Lower Carboniferous (Tournaisian)–Upper Permian.

Genera Included.—*Martiniopsis* Waagen, 1883 [= *Roespirifer* Waterhouse and Piasin, 1970]; *Arktikina* Grunt, 1977; *Crassumbo* Carter, 1967; *Nodaea* Tachibana, 1981.

Family Ingellarellidae Campbell, 1959

[*nom. transl.* Archbold and Thomas, 1986, p. 582,

ex Ingellarellinae Campbell, 1959, p. 333]

Diagnosis.—Micro-ornament of quincuncially arranged elongate grooves and ridges; ventral interior with dental adminicula.

Discussion.—The genera in this family are differentiated and assigned to subfamilies on the basis of micro-ornament, the nature of which is poorly known for

several genera. Reassignment or synonymizing of one or more genera is likely to be necessary.

Stratigraphic Range.—Lower Carboniferous (Viséan)—Upper Permian.

Subfamily Ingelarellinae Campbell, 1959

[Subfamily Ingelarellinae Campbell, 1959, p. 333]

Diagnosis.—Spinules absent; dorsal adminicula well developed.

Discussion.—*Ambikella* Sahni and Srivastava is based on a single, poorly preserved specimen and its validity has not been confirmed.

Stratigraphic Range.—Lower Carboniferous (Viséan)—Upper Permian.

Genera Included.—*Ingelarella* Campbell, 1959; ?*Ambikella* Sahni and Srivastava, 1956; *Fredericksia* Paeckelmann, 1931; *Tabellina* Waterhouse, 1986; *Tomiopsis* Benediktova, 1956 [= *Danzania* Pavlova, 1989].

Subfamily Notospiriferinae Archbold and Thomas, 1986

[Subfamily Notospiriferinae Archbold and Thomas, 1986, p. 584]

Diagnosis.—Fold and sulcus well developed; micro-ornament of quincuncially arranged grooves and ridges, with anteriorly directed spinules at posterior ends of short grooves, and with deep elongate globose pits extending into secondary layer under spinules; dorsal adminicula short or absent.

Stratigraphic Range.—Upper Carboniferous or Lower Permian—Upper Permian.

Genera Included.—*Notospirifer* Harrington, 1955; *Farmerella* Clarke, 1992.

Subfamily Glendoniinae Clarke, 1992

[Subfamily Glendoniinae Clarke, 1992, p. 75]

Diagnosis.—Micro-ornament of quincuncially arranged shallow elongate grooves terminated anteriorly by low elongate spinules and shallow elongate pits.

Stratigraphic Range.—Permian (Asselian–Kazanian).

Genera Included.—*Glendonia* McClung and Armstrong, 1978; *Birchsella* Clarke, 1987; *Homevalaria* Waterhouse, 1986; *Kelsovia* Clarke, 1990.

Family Gerkispiridae Carter, 1985

[Family Gerkispiridae Carter, 1985, p. 376]

Diagnosis.—Ovate to transverse; lateral slopes costate; hingeline short; fold-sulcus moderately to well developed; delthyrium with low thin flaring stegidial plates; ventral interior with short thin dental adminicula, commonly with low apical myophragm; dorsal interior with short converging crural plates and small ctenophoridium; micro-ornament of quincuncially arranged very fine uniramous hollow spinules or papillae that originate in fibrous layer.

Discussion.—The genus *Spinospirifer* Martynova differs from the other genera assigned here in having a widely hinged growth form, a single row of spine bases along each plica, and a weakly capillate micro-ornament. It is tentatively placed here due to its spinose ornament and impunctate shell substance.

Stratigraphic Range.—Upper Devonian (Lower Famennian)—Lower Carboniferous (Tournaisian).

Genera Included.—*Gerkispira* Carter, 1983; *Acanthospirina* Schuchert and LeVene, 1929; *Oiosia* Cooper and Dutro, 1982; *Punctothyris* Hyde, 1953; ?*Spinospirifer* Martynova, 1961.

Family Perissothyrididae Carter, **new family**

Diagnosis.—Subequally biconvex; transversely subovate; low concave interareas present in both valves; fold moderately developed; sulcus weak, shallow, poorly delimited; lateral slopes with weak simple ribbing; micro-ornament absent; delthyrium very wide, partially occluded apically by “pseudodelthyrial plate” (fused dental flanges?); dental adminicula absent; wide dorsally reflexed dental flanges directed medially; large ctenophoridium supported by short median ridge; crural bases medially directed, with ventrally reflexed medial flanges.

Stratigraphic Range.—Lower Carboniferous.

Genera Included.—*Perissothyris* Carter, 1967; *Mongoliopsis* Grunt, 1977.

Superfamily Spiriferoidea King, 1846

[*nom. correct.* Carter, herein

(*pro* Superfamily Spiriferacea King, 1846, p. 28;

nom. transl. Schuchert, 1896, p. 333, *ex* Spiriferidae King, 1846, p. 28)]

Diagnosis.—Ventral beak incurved, ventral interarea low, usually apsacline; hingeline denticulate except in genera with very narrow hingeline; fold and sulcus usually ribbed; ctenophoridium present; prismatic shell layer present in some genera.

Discussion.—Following Ivanova (1981), the impunctate paeckelmanellids are placed in their own superfamily, the Paeckelmanelloidea. In the previous Treatise classification, Pitrat (1965) placed the genera in this superfamily in the punctate superfamilies Syringothyridoidea and Spiriferinoidea. Also, all punctate genera have been removed from the Spiriferoidea and are now included in the Order Spiriferinida.

This superfamily is severely restricted herein to include only families believed to have been derived from a common ancestor in the Late Devonian. Besides the paeckelmanellids the brachythyridids have been removed from the Spiriferoidea. The brachythyridids are believed to have been derived from a Late Devonian theodossioid ancestral stock that diverged from the line that gave rise to the Spiriferoidea and Paeckelmanelloidea. The Paeckelmanelloidea and Spiriferoidea are judged to have arisen from the same indeterminate theodossioid lineage. This hypothetical theodossioid ancestor may have been strophic, at least partially denticulate, capillate or modified capillate, bearing dental adminicula, and carrying the tendency to produce a prismatic shell layer.

Stratigraphic Range.—Upper Devonian (Famennian)—Upper Permian.

Family Spiriferidae King, 1846

[Family Spiriferidae King, 1846, p. 28]

Diagnosis.—Outline variable; hingeline coarsely denticulate except for narrow areas near delthyrium; delthyrial cover weakly developed or absent; lateral slopes and fold-sulcus costate to costellate; micro-ornament capillate; short delthyrial plate variably developed; dorsal adminicula or crural plates not developed; vascular impressions absent or simple.

Discussion.—This family contains two of the earliest appearing members of the Spiriferoidea, the late Famennian genera *Paralellora* Carter, 1974, of the Subfamily Prospirinae, and *Eobrachythyris* Brice 1971, of the Subfamily Sergospiriferinae. *Eobrachythyris* is most similar to the theodossioids in growth form and macro-ornamentation and could be considered to be closest to a hypothetical ancestor for this superfamily. Such a likely theodossioid ancestor might be *Palaeospirifer*

Martynova and Sverlibova, 1968, except that it lacks any indication of a denticulate or partially denticulate hingeline.

Stratigraphic Range.—Upper Devonian (Famennian)—Upper Permian.

Subfamily Spiriferinae King, 1846
[*nom. transl.* Waterhouse, 1968, p. 9,
ex family Spiriferidae King, 1846, p. 28]

Diagnosis.—Cardinal extremities extended in juveniles; outline variable in adults; flanks and fold-sulcus with numerous costae that commonly bifurcate; fold usually poorly delimited; dental adminicula usually developed, and when present, moderately divergent.

Discussion.—The oldest representatives of this subfamily appear in the late Middle Tournaisian. They were probably derived from a prospirin with a tendency for bifurcation of the ribs such as *Paralellora* or *Unispirifer*. The earliest species of the genus *Spirifer*, *Spirifer gregeri* Weller, 1914, first appears in the Middle Tournaisian of North America. However, wide and narrow hinged species of the genus *Spirifer* appear virtually simultaneously only slightly later in Western Alberta.

Stratigraphic Range.—Lower Carboniferous (Middle Tournaisian)—Upper Permian.

Genera Included.—*Spirifer* (*Spirifer*) Sowerby, 1818; *Spirifer* (*Grandispirifer*) Yang, 1959; *Spirifer* (*Mesochorispira*) Carter, 1992; *Etochoristites* Campbell, 1957; *Larispirifer* Enokjan and Poletaev, 1986; *Latispirifer* Archbold and Thomas, 1985; *Warsawia* Carter, 1974.

Subfamily Prospirinae Carter, 1974
[Subfamily Prospirinae Carter, 1974, p. 680]

Diagnosis.—Cardinal extremities extended in juveniles; growth form variable in adults; lateral slopes with relatively few, mostly simple costae; median sulcal costa usually simple or bifurcating once; lateral sulcal costae usually simple, not numerous, derived from sulcus-bounding costae; fold clearly delimited from lateral slopes by bounding interspaces; dental adminicula usually well developed; ventral umbonal callus commonly present.

Discussion.—The early growth stages of *Andreaspira* Abramov and Grigor'eva, *Austrochoristites* Roberts, and *Kasakhstania* Beznosova are poorly known. Large juveniles or young adults of these genera are strongly transverse as seen from illustrations of the growth lines of mature adult specimens. In the absence of definitive information concerning their early development, their assignment here is tentative.

Stratigraphic Range.—Upper Devonian (Upper Famennian)—Upper Carboniferous (Upper Serpukhovian, ?Moskavian).

Genera Included.—*Prospira* Maxwell, 1954; ?*Andreaspira* Abramov and Grigor'eva, 1986; ?*Austrochoristites* Roberts, 1971; *Finospirifer* Ying, 1979; ?*Kasakhstania* Beznosova, 1968; *Kinghiria* Litvinovich, 1966; *Paralellora* Carter, 1974; *Subspirifer* Shan and Zhao, 1980; *Unispirifer* Campbell, 1957 [= ?*Lytha* Frederiks, 1924].

Subfamily Sergospiriferinae Carter, **new subfamily**

Diagnosis.—Cardinal extremities rounded in juveniles; outline variable in adults; lateral slopes with few, simple or bifurcating costae; lateral sulcal costae usually

simple, derived from bounding costae; fold usually well delimited by bounding interspaces; dental adminicula well developed.

Discussion.—The nature of the hingeline and micro-ornament of *Afghanospirifer* Plodowski are poorly known. If it should prove to be nondenticulate, then it might be related to the Palaeochoristididae. The early growth stages of the type species of *Eobrachythyris* Brice are too poorly known to be certain that they are rounded in all stages. If the cardinal extremities of juveniles of this species prove to be extended, this genus should be reassigned to the Prospirinae.

Stratigraphic Range.—?Upper Devonian (Upper Famennian); Lower Carboniferous (Lower Tournaisian)—Upper Carboniferous; ?Permian.

Genera Included.—? *Afghanospirifer* Plodowski, 1968; *Anthracospirifer* Lane, 1963 [= ? *Plicatocyrtia* Gauri, 1965]; *Cancellospirifer* Campbell, 1953; ? *Eobrachythyris* Brice, 1970; *Eochoristitella* Qi, 1983; *Sergospirifer* Ivanova, 1952.

Subfamily Purdonellinae Poletaev, 1986

[*nom. nov.* Poletaev, 1986, p. 65

(*pro* Subfamily Munellinae Frederiks, 1924, p. 313)]

Diagnosis.—Outline brachythyridid; hingeline narrow; fold and sulcus moderately to well developed, multicostate, not delineated by discontinuity in ribbing; costae on lateral slopes often flattened, simple or subfasciculate; ventral interior with delthyrial plate and diverging dental adminicula; vascular impressions indistinct.

Discussion.—The multicostate freely bifurcating ornament of this group suggests that it is probably derived from the Spiriferinae by neotenous retention of an ovate growth form throughout ontogeny. *Mirifusella* Carter is placed here with considerable doubt. Its simple ribbing and sharply delimited fold are not usual for this subfamily.

Stratigraphic Range.—Lower Carboniferous (Tournaisian)—Lower Permian.

Genera Included.—*Purdonella* Reed, 1944; *Ala* Nalivkin, 1979; *Domokhotia* Abramov and Grigor'eva, 1983; *Eliva* Frederiks, 1924; ? *Mirifusella* Carter, 1971; *Neomunella* Ozaki, 1931; *Podtsheremia* Kalashnikov, 1966.

Family Choristitidae Waterhouse, 1968

[*nom. transl.* Ivanova, 1972, p. 40,

ex Subfamily Choristitidinae Waterhouse, 1968, p. 9]

Diagnosis.—Cardinal extremities rounded in juveniles, variable in large adults; denticulation usually well developed; numerous simple or bifurcating costae usually present on entire surface; micro-ornament capillate; delthyrial plate absent; distinctive vascular impressions commonly present, especially in younger genera.

Stratigraphic Range.—Lower Carboniferous—Permian.

Subfamily Angiospiriferinae Legrand-Blain, 1985

[Subfamily Angiospiriferinae Legrand-Blain, 1985, p. 574]

Diagnosis.—Dental adminicula short and close-set or absent; vascular impressions ramiform, or weakly to moderately reticulate; micro-ornament finely cancellate or radially granulose, formed by weak capillae and fine, slightly lamellose growth lines.

Discussion.—This subfamily first appears in the Visean of Eurasia and North Africa and was undoubtedly derived from some member of the Sergospiriferinae by the acquisition of short dental adminicula, distinct vascular impressions, and

weakly capillate micro-ornament. The assignment of *Quizhouspirifer* Xian is tentative because the vascular impressions are unknown.

Stratigraphic Range.—Lower Carboniferous (Visean)—Lower Permian.

Genera Included.—*Angiospirifer* Legrand-Blain, 1985; *Anthracothyryna* Legrand-Blain, 1984; *Brachythyryna* Frederiks, 1929 [= *Anelasmina* Semikhatova, 1939]; *Elinoria* Cooper and Muir-Wood, 1951; *Eobrachythyryna* Lazarev and Poletaev, 1982; *Prochoristitella* Legrand-Blain, 1969; ?*Quizhouspirifer* Xian, 1982.

Subfamily Choristitinae Waterhouse, 1968

[Subfamily Choristitidinae Waterhouse, 1968, p. 9]

Diagnosis.—Dental adminicula close-set, subparallel; vascular impressions reticulate.

Discussion.—*Settedabania* Abramov has an unusual muscle platform in the ventral valve and lacks any indication of vascular markings.

Stratigraphic Range.—?Lower Carboniferous; Upper Carboniferous; ?Lower Permian.

Genera Included.—*Choristites* Fischer de Waldheim, 1825 [= *Alphachoristites* Gatinaud, 1949; ?*Betachoristites* Gatinaud, 1949; *Yatsengina* Semikhatova, 1936]; *Choristitella* Ivanov and Ivanova, 1937; *Parachoristites* Barkhatova, 1968; ?*Settedabania* Abramov, 1970; *Trautscholdia* Ustritsky, 1967.

Subfamily Tangshanellinae Carter, new subfamily

Diagnosis.—Outline subovate with rounded cardinal extremities; dental and dorsal adminicula absent; vascular impressions poorly developed or unknown.

Discussion.—The coarse simple lateral plicae of *Capillispirifer* Zhang are not characteristic of this subfamily.

Stratigraphic Range.—Upper Carboniferous—Upper Permian.

Genera Included.—*Tangshanella* Chao, 1929; *Alphaneospirifer* Gatinaud, 1949 [= *Semibrachythyryna* Yang, 1962]; ?*Capillispirifer* Zhang, 1983; *Zhejiangospirifer* Liang, 1982.

Family Imbrexiidae Carter, 1992

[Family Imbrexiidae Carter, 1992, p. 327]

Diagnosis.—Outline transversely subquadrate; cardinal extremities extended in juveniles, variable in adults; fold and sulcus well developed, often medially subangular, flaring anteriorly in some genera; ventral interior with dental adminicula and short delthyrial plate; ornament of moderately numerous simple or bifurcating costae on both flanks and fold-sulcus; micro-ornament of weak capillae and regularly imbricate growth lamellae.

Discussion.—Carter (1992:328) speculated that this family was derived from the Prospirinae because of similarities in macro- and micro-ornament between prospirins and the earliest imbrexiid genus *Fernglenia* Carter.

Stratigraphic Range.—Lower Carboniferous (?Middle, Upper Tournaisian).

Genera Included.—*Imbrexia* Nalivkin, 1937; *Fernglenia* Carter, 1992; *Tegulocrea* Carter, 1992.

Family Trigonotretidae Schuchert, 1893

[*nom. transl.* Carter, herein,

ex Subfamily Trigonotretinae Schuchert, 1893, p. 156]

Diagnosis.—Usually strongly transverse in adult growth stage; fold and sulcus

well developed; denticulate hingeline well developed; entire surface ribbed, often plicate; lateral slopes commonly fasciculate.

Stratigraphic Range.—Lower Carboniferous–Upper Permian.

Subfamily Neospiriferinae Waterhouse, 1968
[Subfamily Neospiriferinae Waterhouse, 1968, p. 9]

Diagnosis.—Weakly to strongly fasciculate; costae medium to fine, nearly uniform in size anteriorly; micro-ornament weakly capillate, often lamellose or imbricate; ventral interior with delthyrial plate.

Discussion.—The genus *Blasispirifer* Kulikov is placed here tentatively on the basis of having a few fasciculate plicae. In addition, its growth form and lack of dental adminicula are not usual for this subfamily. The neospiriferins are likely to have been derived from the Imbrexiidae by acquisition of fasciculate plicae on the flanks.

Stratigraphic Range.—Upper Carboniferous–Upper Permian.

Genera Included.—*Neospirifer* Frederiks, 1924; *Betaneospirifer* Gatinaud, 1949; ?*Blasispirifer* Kulikov, 1950; *Cartorhium* Cooper and Grant, 1976; *Costatospirifer* Archbold and Thomas, 1985; *Crassispirifer* Archbold and Thomas, 1985; *Cratispirifer* Archbold and Thomas, 1985; *Fusispirifer* Waterhouse, 1966 [= *Transversaria* Waterhouse and Gupta, 1983]; *Gibbospirifer* Waterhouse, 1971; *Gypospirifer* Cooper and Grant, 1976; *Imperiospira* Archbold and Thomas, 1993; *Kaninospirifer* Kulikov and Stepanov, 1975; *Lepidospirifer* Cooper and Grant, 1969; *Pondospirifer* Waterhouse, 1978; *Septospirifer* Waterhouse, 1971; *Tibetospirifer* Liu and Wang, 1990.

Subfamily Trigonotretinae Schuchert, 1893
[Subfamily Trigonotretinae Schuchert, 1893, p. 156]

Diagnosis.—Transverse; often thick shelled; fold and sulcus moderately developed; lateral slopes weakly to strongly plicate, variable fasciculate; finer ribbing medium to coarse, often forming unequal ribs anteriorly; micro-ornament capillate and variably cancellate; ventral interior with dental adminicula, obscured by thick apical, commonly bulbous, delthyrial callus.

Discussion.—*Brachythyridella* Waterhouse and Gupta is tentatively assigned here on the basis of its macro-ornament, which is well illustrated in Thomas (1971:pl. 19). Internally, it differs greatly from the other genera placed here, lacking a delthyrial plate or umbonal callus. *Sulciplica* Waterhouse does not have secondary costae or costellae imposed on the plicae and thus differs from the other genera in this subfamily.

Stratigraphic Range.—Lower Carboniferous (Visean)–Upper Permian.

Genera Included.—*Trigonotreta* Koenig, 1825 [= *Grantonia* Brown, 1953]; *Aperispirifer* Waterhouse, 1968; ?*Brachythyridella* Waterhouse and Gupta, 1978; *Frechella* Legrand-Blain, 1986; ?*Sulciplica* Waterhouse, 1968.

Family Spiriferellidae Waterhouse, 1968
[*nom. transl.* Carter, herein,

ex Subfamily Spiriferellinae Waterhouse, 1968, p. 9]

[=Family Spiriferellidae Termier, Termier, Lapparant, and Martin, 1974, p. 136]

Diagnosis.—Lateral slopes plicate, coarsely costate, or fasciculate; fold usually with median furrow; delthyrium commonly partially or completely occluded by convex stegidial plates; denticulation poorly developed in narrow hinged genera;

micro-ornament pustulose, commonly capillate; ventral interior with strong short dental adminicula; ventral umbonal region often greatly thickened by callus with deeply impressed ventral muscle field.

Discussion. — *Spiriferellaoides* Lee, Gu, and Li is based on a single poorly preserved specimen. Although it is very difficult to evaluate, it may prove to be a junior synonym of *Spiriferella* and for this reason its assignment here is questioned. *Tipispirifer* Grant is truly enigmatic. Its growth form and macro-ornament of fine costae are unusual for this family. It is assigned here on the basis of its pustulose micro-ornament and stegidial cover of the delthyrium.

The other genera in this family form a close-knit group characterized by thick ventral umbones and a pustulose micro-ornament. They were probably derived from the Trigonotretinae by the acquisition of pustulose micro-ornament.

Stratigraphic Range. — Upper Carboniferous (Bashkirian)–Upper Permian (Vedrian).

Genera Included. — *Spiriferella* Chernyshev, 1902; *Alispiriferella* Waterhouse and Waddington, 1982; *Arcullina* Waterhouse, 1986; *Elivina* Frederiks, 1924; *Eridmatus* Branson, 1966; *Plicatospiriferella* Waterhouse and Waddington, 1982; *Rhomboispirifer* Duan and Li, 1985; ?*Spiriferellaoides* Lee, Gu, and Li, 1980; *Timaniella* Barkhatova, 1968; ?*Tipispirifer* Grant, 1976.

Superfamily Paeckelmanelloidea Ivanova, 1972

[*nom. correct.* Carter, herein

(*pro* Paeckelmanellacea Ivanova, 1981, p. 22) *nom. trans.* Ivanova, 1981, p. 22, *ex* Paeckelmanellidae Ivanova, 1972, p. 40]

Diagnosis. — Moderately to strongly transverse with maximum width at hingeline; ribs usually simple on flanks, but geologically younger forms sometimes with bifurcations; fold and sulcus smooth or with median rib in sulcus, or more rarely, multicostate; ventral interarea usually moderately to very high, often catacline to slightly procline or weakly apsacline; hingeline denticulate; micro-ornament consisting of capillae and anteriorly free growth lamellae; dental adminicula usually present; vascular markings simple, radial; ctenophoridium present.

Discussion. — The origin of this superfamily is not certain, but it clearly began in the Famennian. The earliest paeckelmanelloid, *Strophopleura* Stainbrook, appeared in the early Upper Famennian, slightly before the earliest true spiriferoids *Parallelora* or *Eobrachythyris*. The denticulate hingeline and capillate micro-ornament point to a close relationship with the Spiriferoidea, probably a shared ulbospiriferid ancestor.

Stratigraphic Range. — Upper Devonian–Upper Permian.

Family Strophopleuridae Carter, 1974

[*nom. trans.* Carter, herein, *ex* Strophopleurinae Carter, 1974, p. 677]

Diagnosis. — Ventral septum absent.

Stratigraphic Range. — Upper Devonian–Upper Permian.

Subfamily Strophopleurinae Carter, 1974

[Subfamily Strophopleurinae Carter, 1974, p. 677]

Diagnosis. — Small, with simple lateral ribs; sulcus smooth or with median rib.

Discussion. — *Calvustrigis* Carter is tentatively placed here because it lacks an imbricate ornament, differing from all other genera assigned here. Although *Iwaispirifer* Tachibana is poorly known and a denticulate hingeline has not been

established, its growth form, close-set dental adminicula, and imbricate-capillate micro-ornament strongly suggest placement here.

Stratigraphic Range.—Upper Devonian (Famennian)—Upper Carboniferous (Moscovian).

Genera Included.—*Strophopleura* Stainbrook, 1947; *Acuminothyris* Roberts, 1963; *Avisyrinx* Martinez Chacon, 1975; ?*Calvustrigis* Carter, 1987; *Cantabriella* Martinez Chacon and Rio Garcia, 1987; ?*Iwaispirifer* Tachibana, 1963; *Voiseyella* Roberts, 1964 [= *Amesopleura* Carter, 1967].

Subfamily Bashkiriinae Nalivkin, 1979

[*nom. trans.* Carter, herein, *ex* Bashkiriidae Nalivkin, 1979, p. 143]

Diagnosis.—Small to medium size; lateral ribs simple; fold and sulcus ribbed; ventral interarea moderately high to very high, often flattened, catacline to procline.

Discussion.—Denticulation in the genus *Adminiculoria* Waterhouse and Gupta has not been established; otherwise, it could be assigned here confidently.

Stratigraphic Range.—Lower Carboniferous.

Genera Included.—*Bashkiria* Nalivkin, 1979; ?*Adminiculoria* Waterhouse and Gupta, 1978; *Celsifornix* Carter, 1974; *Fusella* McCoy, 1844.

Subfamily Pterospiriferinae Waterhouse, 1975

[Subfamily Pterospiriferinae Waterhouse, 1975, p. 15]

Diagnosis.—Medium sized to large; ribs on flanks simple or bifurcating, rarely fasciculate; fold and sulcus smooth or with median rib, rarely costate; dental adminicula short and divergent.

Stratigraphic Range.—Upper Carboniferous—Upper Permian.

Genera Included.—*Pterospirifer* Dunbar, 1955; *Alispirifer* Campbell, 1961; *Haplospirifer* Lee and Gu, 1976; *Pteroplecta* Waterhouse, 1978; *Spiriferinaella* Frederiks, 1926; *Xizispirifer* Liang, 1990.

Family Paeckelmanellidae Ivanova, 1972

[Family Paeckelmanellidae Ivanova, 1972, p. 40]

Diagnosis.—With ventral medium septum; lateral ribs simple.

Stratigraphic Range.—Lower Permian—Upper Permian.

Subfamily Paeckelmanellinae Ivanova, 1972

[*nom. trans.* Waterhouse, 1975, p. 15,

ex Paeckelmanellidae Ivanova, 1972, p. 40]

Diagnosis.—With short divergent dental adminicula.

Stratigraphic Range.—Lower Permian—Upper Permian.

Genera Included.—*Paeckelmanella* Likharev, 1934; *Darvasia* Likharev, 1934; *Odontospirifer* Dunbar, 1955.

Subfamily Scenesiinae Carter, **new subfamily**

Diagnosis.—With short apical delthyrial plate; dental adminicula absent.

Stratigraphic Range.—Lower Permian.

Genus Included.—*Scenesia* Cooper and Grant, 1976.

Superfamily Brachythyridoidea Frederiks, 1924

[*nom. transl.* Carter, herein

(*ex* Brachythyrinae Frederiks, 1924, p. 316)]

Diagnosis. — Outline ovate; hingeline narrow; cardinal extremities rounded in all growth stages; lateral slopes with coarse, usually simple ribbing; fold-sulcus weakly to moderately developed; denticulation not present in younger genera; micro-ornament absent or weakly developed; dental adminicula, subdelthyrial plate, and dorsal adminicula absent; delthyrium partially covered by thin deltidium or stegidial plates.

Discussion. — The suppressed denticulation and lack of capillate micro-ornament suggest that this group may have been derived independently from the theodossoids or an intermediate ancestor by neoteny, with concomitant loss of dental adminicula.

The origin of this superfamily is obscured by the pedomorphically simple internal morphology of the genera included here. Also, the characteristic rounded outline and general absence of micro-ornament of these genera could be construed as either primitive or derived. Assuming that at least some of these characters give an indication of ancestry, it seems possible that this group was derived from a subovate, well-inflated form with a few coarse simple ribs on each lateral slope. Because there is weak denticulation of the hingeline and obscurely capillate micro-ornament in at least one of the geologically early genera, it seems most likely that this group was derived from an offshoot of the same stock that produced the other Late Paleozoic superfamilies of this order, namely, the Theodossioidea.

Stratigraphic Range. — Upper Devonian (Famennian)–Permian.

Family Brachythyrididae Frederiks, 1924

[*nom. transl. et correct.* Pitrat, 1965, p. H706,
ex Subfamily Brachithyrinae Frederiks, 1924, p. 316]

Diagnosis. — Primary median costa in sulcus absent.

Discussion. — *Dalaia* Plodowski was originally assigned by Plodowski (1968: 256) to the Reticulariidae, but it lacks spinose or pitted ornament and cannot be assigned to either the Reticularioidea or Martinioidea. The micro-ornament of *Pustulosplica* Waterhouse consists of discontinuous capillae and elongated fine nodes or pustules, which is unknown in other members of this superfamily. This micro-ornament is reminiscent of several martiniid genera and assignment of *Pustuloplica* here is uncertain.

Stratigraphic Range. — Upper Devonian (Famennian)–Permian (?Kazanian).

Genera Included. — *Brachythyris* McCoy, 1844 [= *Ovalia* Nalivkin, 1937]; *Cathayspirina* Liang, 1990; ?*Dalaia* Plodowski, 1968; *Ella* Frederiks, 1918; *Meristorygma* Carter, 1974; ?*Pustuloplica* Waterhouse, 1968.

Family Skelidorygmidae Carter, **new family**

Diagnosis. — Sulcus with primary median costa, often with additional sulcal costae that bifurcate from sulcus-bounding ribs.

Stratigraphic Range. — Upper Devonian (Famennian)–Upper Carboniferous (Bashkirian).

Genera Included. — *Skelidorygma* Carter, 1974; *Litothyris* Roberts, 1971.

Suborder Delthyridina Ivanova, 1972

[Suborder Delthyridina Ivanova, 1972, p. 41]

Diagnosis. — Lateral slopes plicate, rarely costate; concentric lamellae, if present, fimbriate, spinulose, or exopunctate; early forms with internal plates and septa, tending to become pedomorphically simple in some geologically younger forms; commonly with ctenophoridium.

Stratigraphic Range.—Lower Silurian–Upper Permian.

Superfamily Delthyridoidea Phillips, 1841

[*nom. transl.* Ivanova, 1959, p. 56, *nom. correct.* Johnson, 1970, p. 184
(*ex* Delthyridae Phillips, 1841, p. 54)]

Diagnosis.—Biconvex, with fold and sulcus.

Stratigraphic Range.—Lower Silurian (Upper Llandoveryan)—Middle Devonian (Eifelian).

Family Delthyrididae Phillips, 1841

[*nom. correct.* Johnson, 1970, p. 184
(*pro* Delthyridae Phillips, 1841, p. 54)]

Diagnosis.—Small to medium size, pauciplicate; commonly with crural plates.

Stratigraphic Range.—Lower Silurian (Upper Llandoveryan)—Middle Devonian (Eifelian).

Subfamily Delthyridinae Phillips, 1841

[*nom. transl., nom. correct.* Johnson, 1970, p. 184
(*ex* Delthyridae Phillips, 1841, p. 54)]

Diagnosis.—Ventral median septum present.

Stratigraphic Range.—Upper Silurian (Wenlockian)—Middle Devonian (Eifelian).

Genera Included.—*Delthyris* (*Delthyris*) Dalman, 1828; *Delthyris* (*Quadrifarius*) Fuchs, 1929; *Ivanothyris* Havlíček, 1957.

Subfamily Howellellinae Johnson and Hou, **new subfamily**

Diagnosis.—Ventral median septum lacking.

Stratigraphic Range.—Lower Silurian (Upper Llandoveryan)—Middle Devonian (Eifelian).

Genera Included.—*Howellella* (*Howellella*) Kozłowski, 1946; *Howellella* (*Hysterohowellella*) Carls, 1985; *Howellella* (*Iberohowellella*) Carls, Meyn, and Vespermann, 1993; *Acanthospirifer* Menakova, 1964; *Aldanispirifer* Alekseeva, 1967 [= *Holcospirifer* Bassett, Cocks, and Holland, 1976]; *Howelloidea* Su, 1980; *Orientospirifer* Hou and Xian, 1975; *Pseudokymatothyris* Chen, 1979; *Qiansispirifer* Yang, 1977; *Rufispirifer* Havlíček, 1987; *Xenospirifer* Hou and Xian, 1975.

Family Hysterolitidae Termier and Termier, 1949

[*nom. transl.* Johnson and Hou herein
(*ex* Hysterolitinae Termier and Termier, 1949, p. 95)]

Diagnosis.—Medium to large size; fold and sulcus smooth or plicate; flanks commonly multiplicate; crural plates present or absent.

Stratigraphic Range.—Lower Devonian (Upper Lochkovian)—Middle Devonian (Lower Givetian).

Subfamily Hysterolitinae Termier and Termier, 1949

[Hysterolitinae Termier and Termier, 1949, p. 95]
[=Paraspiriferinae Pitrat, 1965, p. H684]

Diagnosis.—Fold and sulcus smooth; mostly lacking crural plates.

Stratigraphic Range.—Lower Devonian (Upper Lochkovian)—Middle Devonian (Eifelian).

Genera Included.—*Hysterolites* Schlotheim, 1820; *Antispirifer* Williams and Breger, 1916; *Arduspirifer*, Mittmeyer, 1972; *Australospirifer* Caster, 1939; *Brachyspirifer* (*Brachyspirifer*) Wedekind in Salomon, 1926; *Brachyspirifer* (*Torosospirifer*) Gourvennec, 1989; *Costellispirifer* Boucot, 1973 [= *Concinnispirifer* Boucot, 1975]; *Dixonella* Gourvennec, 1989; *Dyticospirifer* Johnson, 1966; *Euryspirifer* Wedekind in Salomon, 1926 [= *Rhenospirifer* Mittmeyer, 1972]; *Otospirifer* Hou and Xian, 1975; *Paraspirifer* Wedekind, 1926; *Patriaspirifer* Johnson, 1995; *Rostrospirifer* Grabau, 1931 [= *Neodelthyris* Hou, 1963]; *Trigonospirifer* Wang, Rong, and Chen, 1987; *Xinjiangospirifer* Hou and Zhang, 1983.

Subfamily Fimbrispiriferinae Pitrat, 1965

[*nom. transl.* Wang, 1979, p. 77

(*ex* Fimbrispiriferidae Pitrat, 1965, p. H687)]

Diagnosis.—Fold, sulcus, and flanks plicate; crural plates present or absent.

Discussion.—Boucot (1975) proposed *Vandercammenina* and *Struveina* as Old World-Realm genera of the Acrospiriferinae, but they are here excluded from that subfamily because of their fimbriate ornament. We regard *Fimbrispirifer*, a Middle Devonian genus from eastern North America, as a descendant of *Struveina* by late migration of that stock, following a pattern demonstrated for the genus *Paraspirifer* (Johnson, 1979).

Stratigraphic Range.—Lower Devonian (Pragian)—Middle Devonian (Lower Givetian).

Genera Included.—*Fimbrispirifer* Cooper, 1942; *Struveina* Boucot, 1975; *Vandercammenina* Boucot, 1975.

Family Acrospiriferidae Termier and Termier, 1949

[*nom. transl.* Johnson and Hou herein

(*ex* Acrospiriferinae Termier and Termier, 1949, p. 96)]

Diagnosis.—Medium to large size, transverse, capillate with fila; crural plates present or absent.

Discussion.—A peculiarity of genera in this family is the presence of fine or prominent capillae together with a concentric ornament of fila. Examples are *Acrospirifer primaevus* as illustrated by Vandercammen (1963:pl. 1, fig. 19, pl. 2, fig. 11), *Acrospirifer fallax* as illustrated by Jahnke (1971:pl. 6, fig. 10), and *Mauispirifer hectori* as illustrated by Allan (1947:pl. 62, fig. 6). Capillae are so well developed on *Multispirifer* that it was originally presumed to be an eospiriferid (Kaplun, 1961:88). The capillae of *Costispirifer* caused Ivanova (1972) to suppose that it was derived from the eospiriferids. Of particular interest is the ornament of *Euryspirifer* Wedekind, 1926. Vandercammen (1963:pl. 8, fig. 6) and Jahnke (1971:pl. 7, fig. 4c) both show an ornament of capillae interrupted by fila. This type of ornament is especially well represented by *Euryspirifer atlanticus*, as illustrated by Boucot (1973:pl. 17, fig. 9).

Stratigraphic Range.—Lower Devonian (Upper Lochkovian)—Middle Devonian (Eifelian).

Subfamily Acrospiriferinae Termier and Termier, 1949

[Acrospiriferinae Termier and Termier, 1949, p. 96]

Diagnosis.—Flanks strongly plicate, delthyrium lacking apical deltidium; dental plates strong or partly buried in umbonal callus; ctenophoridium on floor of notothyrial chamber attached to myophragm, or elevated.

Stratigraphic Range.—Lower Devonian (Upper Lochkovian–Emsian).

Genera Included.—*Acrospirifer* Helmbrecht and Wedekind, 1923; *Mauispirifer* Allan, 1947; *Xerospirifer* Havlíček, 1978.

Subfamily Costispiriferinae Termier and Termier, 1949

[Costispiriferinae Termier and Termier, 1949, p. 98]

Diagnosis.—Multiplicate, with narrow interspaces; ventral interarea low, trapezoidal; broad delthyrium with apical deltidium; fold and sulcus smooth or plicate; flanks with simple plications; short, widely spaced dental plates, partly buried in umbonal callus; sockets strong, simple, curved; ctenophoridium not built up.

Discussion.—Although *Cumberlandina* was originally assigned to the Mucrospiriferinae by Boucot (1975:371), that assignment cannot be sustained because *Cumberlandina* lacks lamellose concentric ornament. Except for the lack of plications on the fold and sulcus, *Cumberlandina* closely resembles *Costispirifer*.

Stratigraphic Range.—Lower Devonian (Pragian).

Genera Included.—*Costispirifer* Cooper, 1942; *Cumberlandina* Boucot, 1975.

Family Elymospiriferinae Johnson and Hou, **new subfamily**

Diagnosis.—Fold and sulcus plicate; flanks with bifurcating plications.

Stratigraphic Range.—Lower Devonian (Pragian)—Middle Devonian (Eifelian).

Genera Included.—*Elymospirifer* Wang, 1974; *Borealispirifer* Hou and Su, 1993; *Multispirifer* Kaplun, 1961; *Perryspirifer* Jones and Boucot, 1983.

Family Cyrtinopsidae Wedekind, 1926

[*nom. transl.* Boucot, 1957, p. 38

(*ex* Cyrtinopsinae Wedekind in Salomon, 1926, p. 198)]

Diagnosis.—Frilly growth lamellae, with interrupted capillae; ctenophoridium lacking or, in younger genera, rudimentary.

Stratigraphic Range.—Upper Silurian (Wenlockian)—Middle Devonian (Givetian).

Subfamily Cyrtinopsinae Wedekind, 1926

[Cyrtinopsinae Wedekind in Salomon, 1926, p. 198]

[=Kozłowskiellinae Boucot, 1958, p. 1031

(*nom. correct.* Kozłowskiellinae Boucot, 1957, p. 317)]

Diagnosis.—With ventral median septum.

Stratigraphic Range.—Upper Silurian (Wenlockian)—Middle Devonian (Givetian).

Genera Included.—*Cyrtinopsis* Scupin, 1896; *Kozłowskiellina* Boucot, 1958; *Megakozłowskiella* Boucot, 1957; *Plicocyrtina* Havlíček, 1956.

Subfamily Araspiriferinae Johnson, **new subfamily**

Diagnosis.—Without ventral median septum.

Stratigraphic Range.—Upper Silurian (Wenlockian–Ludlovian).

Genera Included.—*Araspirifer* Havlíček, 1987; *Boucotinskia* Brunton and Cocks, 1967.

Family Mucrospiriferidae Boucot, 1959

[*nom. transl.* Johnson and Carter herein

(*ex* Mucrospiriferinae Boucot, 1959, p. 745)]

Diagnosis.—Lamellose growth lines; ctenophoridium without crural plates.

Stratigraphic Range.—Middle Devonian (Givetian)–Lower Carboniferous (Visean).

Subfamily Mucrospiriferinae Boucot, 1959

[Mucrospiriferinae Boucot, 1959, p. 745]

Diagnosis.—Transverse, multiplicate; dental plates present or absent; without median septum.

Stratigraphic Range.—Middle Devonian (Givetian)–Upper Devonian (Famennian).

Genera Included.—*Mucrospirifer* Grabau, 1931 [= *Lamellispirifer* Nalivkin, 1937; *Khinganospirifer* Su, 1976]; *Apousiella* Carter, 1972 [= *Bouchardopsis* Mailleux, 1933]; *Eleutherokomma* Crickmay, 1950 [= *Dmitrispirifer* Liashenko, 1973; *Sculptospirifer* Su, 1980]; *Sulcatospirifer* Maxwell, 1954.

Subfamily Tylothyridinae Carter, 1972

[Tylothyridinae Carter, 1972, p. 730]

Diagnosis.—Variable outline and moderately numerous lateral costae; radial ornament apparently lacking; with dental plates and median septum.

Stratigraphic Range.—Middle Devonian (Upper Givetian)–Lower Carboniferous (Visean).

Genera Included.—*Tylothyris* North, 1920 [= *Welleria* Mailleux, 1931]; *Texathyris* Carter, 1972.

Superfamily Reticularioidea Waagen, 1883

[*nom. correct.* Gourvennec and Carter, herein

(*pro* Reticulariacea Waagen, 1883, *nom. transl.* Pitrat, 1965, p. H717,

ex Subfamily Reticulariinae Waagen, 1883, p. 538)]

Diagnosis.—Subequally biconvex; outline generally transversely subovate to equidimensional; hinge line short, lateral extremities rounded; fold and sulcus generally present, commonly weakly developed; ribbing absent or weak, rarely multicostate; micro-ornament often lamellose, commonly with fine spines or granules.

Stratigraphic Range.—Silurian (Upper Llandovery)–Upper Permian.

Family Reticulariidae Waagen, 1883

[*nom. transl.* Ivanova, 1959, p. 56,

ex Subfamily Reticulariinae Waagen, 1883, p. 538]

Diagnosis.—Lateral slopes commonly smooth, rarely plicate; fold and sulcus, if present, smooth; micro-ornament concentrically arranged, consisting of growth lamellae and generally uniramous spinules or fine tubercles; dental adminicula generally present, true ventral septum absent, median ridge or myophragm present in some genera.

Discussion.—This diagnosis is based on the assumption that *Reticularia* lacks a true ventral septum but, rather, possesses a median ridge or euseptoid, as described and illustrated by George (1932:552). If this is actually not the case, then the following classification is incorrect and we would be compelled to reassign all of the nonseptate genera to a different family and revise the composition of the Xenomartiniidae.

Stratigraphic Range.—Silurian (Upper Llandovery)–Upper Permian.

Subfamily Reticulariinae Waagen, 1883
[Subfamily Reticulariinae Waagen, 1883, p. 538]

Diagnosis.—Generally pauciplicate; lacking delthyrial plates, delthyrial ridges or any kind of apical thickening; commonly lacking crural plates.

Discussion.—Havlíček erected the genus *Undispirifer* in 1957 and designated *S. undiferus* Roemer 1844 as type species. He pointed out the presence of a well-developed fold and sulcus and low lateral plications, which are commonly only perceptible anteriorly. In 1959, he added “basal plates do not meet the floor of the valve” and “without subdelthyrial plate” (in the comparison with *Eoreticularia*). In 1967, Vandercammen gave illustrations of the original material of Roemer, considering *undiferus* and *gerolsteinites* Steininger, 1853, as synonyms (form I and II of the species *undiferus*, p. 6). His figure shows a specimen labeled “Original *Sp. undiferus* F. Roemer” but Vandercammen indicated that this specimen probably is not the type, which was apparently lost (there are effectively some differences with the original illustration by Roemer). The origin of the label is unknown. This specimen seems closely related to the type of *S. curvata undulata* Roemer, 1844 (pl. 4, fig. 5a, b) which was later designated as the type of *S. gerolsteinensis* by Steininger (1853). Recently, Struve (1990) erected the genus *Gerolsteinites*, with *Spirifera gerolsteinensis* Steininger as the type species, and which is distinguished from *Undispirifer* by: 1) a well-marked fold and sulcus, 2) plicae expressed from apex to commissure, and 3) a high ventral interarea. These arguments do not justify the erection of a new genus because the original diagnosis of *Undispirifer* states that there is a well-developed sulcus/fold and lateral plications are often (but not necessarily) only perceptible anteriorly. In addition, the original illustration by Roemer (1844:pl. 4, fig. 6a–c) shows *undiferus* with a well-developed, if not high, ventral interarea, not far in its form from that of *S. gerolsteinensis* (= *S. curvatus undulata*). It is clear that the characters of the genus *Undispirifer* show some variability, but the erection of a new genus does not appear as a necessity (*Gerolsteinites* at most should have subgeneric rank). In any case the problem of the type is not solved. Some other features illustrate the variability in this genus. According to Havlíček (1959:254), *Undispirifer* is devoid of a delthyrial plate. However, some authors have mentioned such a plate, following Vandercammen (1957:6), who indicated that a delthyrial plate is present but difficult to identify. There is a possibility that the specimen described by Vandercammen belongs to another genus, e.g., *Rhenothyris*, because his description of the species states that some large mature specimens are smooth (1957:5). Otherwise, although *Undispirifer* generally lacks crural plates and possesses only plate-like crural bases (Havlíček, 1959:254), it seems that in some specimens these plates join the floor of the valve (Johnson, 1974:pl. 10, fig. 4). The preceding discussion shows that a revision of the species *undiferus* and the designation of a neotype are desirable. Because there is still doubt about the presence or absence of a delthyrial plate, the genus is assigned here with a question mark.

The subgenus *Nakazatothyris* Minato and Kato, 1977 is also placed in synonymy of the genus *Undispirifer* for reasons comparable to the ones mentioned above: its characters (few plicae better expressed in the vicinity of the fold/sulcus and near the apex) do not justify the erection of a (sub-)genus because they fall within a reasonable variation of the genus *Undispirifer*. *Undispiriferoides* Xian is poorly known and its status is not clear.

Stratigraphic Range.—Lower Devonian (Upper Pragian)—Upper Permian.

Genera Included.—*Reticularia* McCoy, 1844; ?*Georgethyris* Minato, 1953;

Parareticularia Lee and Gu, 1976; *Squamularia* Gemmellaro, 1899; ?*Undispirifer* Havlíček, 1957 [=Nakazatothyris Minato and Kato, 1977] [=Gerolsteinites Struve, 1990]; ?*Undispiriferoides* Xian, 1978.

Subfamily Reticulariopsinae Gourvennec, **new subfamily**

Diagnosis.—Generally pauciplicate; lacking delthyrial plates, delthyrial ridges or any kind of apical thickening; dental plates, crural plates and ctenophoridium present.

Discussion.—The serial sections accompanying the original diagnosis of *Paraquadrithyris* are aberrant and probably erroneous. No comments are given by the author about the cardinal process, but the genus is compared with *Tingella* (=Reticulariopsis), which possesses a ctenophoridium. After Hou, the two genera are probably synonyms.

Vandercammen (1958) does not recognize the genus *Reticulariopsis*, which he considers as insufficiently described, but he accepts *Tingella* Grabau, in which he places *R. dereimsi*, the type species of *Reticulariopsis*. Vandercammen assigned two other species to *Tingella* (*reticularioides* and *concentrica*). The material described under the name of *concentrica* by Vandercammen has since been recognized as *Gerothyris eifliana*, while *T. dereimsi* (*sensu* Vandercammen) has been found only in Belgium and differs from the Spanish species described by Oehlert and Oehlert (1901), which lacks a delthyrial plate. Furthermore, the type species of *Tingella*, *T. reticularioides*, apparently also lacks a delthyrial plate. Thus *Tingella* is a junior synonym of *Reticulariopsis* and the interpretation of Vandercammen (delthyrial plate present) is to be rejected (this latter material probably belongs to *Rhenothyris*).

Stratigraphic Range.—Silurian (Wenlock)—Middle Devonian (Givetian).

Genera Included.—*Corylispirifer* Gourvennec, 1989; *Kymatothyris* Struve, 1970 [=Fallaxispirifer, Su 1976]; *Mariaspirifer* Cherksova, 1991; ?*Paraquadrithyris* Yang, 1983; *Padvenia* Breivel and Breivel, 1988; *Proreticularia* Su, 1990; *Prosserella* Grabau, 1910; *Reticulariopsis* Frederiks, 1916 [=Tingella Grabau, 1931]; *Yeothyris* Struve, 1992.

Subfamily Rhenothyridinae Gourvennec, **new subfamily**

Diagnosis.—With delthyrial plate, ridge or ventral apical thickening; dental plates and ctenophoridium present.

Discussion.—*Rhenothyris* does not possess a true delthyrial plate but only clearly expressed subdelthyrial plates or ridges on internal molds. The definition of the genus *Eohowellella* is imprecise and not in accordance with the insufficient illustrations. For example, the “ventral septum” recorded in the diagnosis is absent on the serial sections; if such a septum is really present, *Eohowellella* would better be assigned to the Quadrithyridinae. The comparison with *Howellella* suggests that a ctenophoridium is present although it is not reported in the diagnosis. The mention of a “finely punctate shell” in the description is probably erroneous(?); such a character would remove *Eohowellella* from the Reticularioidea. For all these reasons, *Eohowellella* is assigned here with doubt.

The ctenophoridium is not reported in the diagnosis of *Nordella* and does not appear in serial sections, but the comparison with *Elita* suggests close analogies in the internal structures, and we admit to the presence of a ctenophoridium. Should this not be the case, *Nordella* would be better placed in the Eoreticulariinae.

Puanospirifer is poorly known; many characters have been “estimated” or ex-

trapolated from the author's comparison with *Reticulariopsis* (particularly for internal structures).

The holotype, paratypes, and figured specimens of *Spirinella* were destroyed by fire in 1953. Strusz (1984) has given a new diagnosis and good illustrations of topotype material, but failed to designate a neotype. We propose to designate the specimen "SUP 55596" (Yass Formation, New South Wales), figured in Strusz (1984:fig. 18A–D) as the lectotype for *Spirinella caecistriata* Johnston (type species of the genus *Spirinella*). Apparently, following the serial sections given by Johnston (1941, fig. 2), *Spirinella* possesses incipient delthyrial plates or ridges. Nevertheless, these structures are poorly expressed and they are not reported by Strusz (1984), who revised the species. Consequently, this genus is assigned here with some doubt. If delthyrial plates and an apical thickening are lacking in *Spirinella*, the Reticulariopsinae would be a better receptacle for this genus.

Stratigraphic Range.—Silurian (?Upper Llandovery, Lower Ludlow)–Middle Devonian (Eifelian, ?Lower Frasnian).

Genera Included.—*Rhenothyris* Struve, 1970; *Deltospirifer* Wang and Rong, 1986; ?*Eohowellella* Lopushinskaja, 1976; *Gerothyris* Struve, 1970; *Grebenella* Modzalevskaia and Besnosova, 1992; ?*Nordella* Liaschenko, 1973; *Pseudoundispirifer* Zhang, 1987; ?*Puanospirifer* Jiang, 1978; ?*Spirinella* Johnston, 1941 [= *Ec-tatoglossa* Chu, 1974]; *Warrenella* (*Warrenella*) Crickmay, 1953 [= *Minatothyris* Vandercammen, 1957]; *Warrenella* (*Warrenellina*) Brice, 1982.

Subfamily Obesariinae Gourvennec, new subfamily

Diagnosis.—Smooth; lacking dental plates and ctenophoridium; apical thickening in the ventral valve.

Discussion.—*Quasimartinia* occasionally possesses a sinus on the dorsal valve, which is quite uncommon in the Reticularioidea.

In the original diagnosis of *Uexothyris*, no mention is made of a ctenophoridium, so we consider it to be lacking. Nevertheless, Struve (1992:574) placed this genus in the Tribe Gerothyridini with *Gerothyris* and "*Minatothyris*," both of which possess a ctenophoridium. In the description of the species assigned to *Uexothyris*, the cardinal process is not taken into consideration and no illustration is given. If *Uexothyris* should prove to possess a ctenophoridium, it should be rejected from the Obesariinae and attached to the Rhenothyridinae, hence the question mark in our assignment.

Echinocoeliopsis is assigned here because of its ornament and lack of dental plates, but it is apparently devoid of an apical thickening. Another peculiar feature of this genus is the presence of a bifid shaft supporting the cardinal process. In some respects (size, form, mode of folding, bifid cardinal process) this genus evokes the Ambocoeliidae, particularly *Metaplasia* and allied genera. Otherwise, *Echinocoeliopsis* is only known by a few very small specimens.

Stratigraphic Range.—Silurian (Upper Wenlock)–Middle Devonian (Eifelian).

Genera Included.—*Obesaria* Havlíček, 1957; *Alaskospira* Kirk and Amsden, 1952 [= *Proreticularia* Havlíček, 1957]; *Quasimartinia* Havlíček, 1959 [= *Candispirifer* Havlíček, 1971]; ?*Uexothyris* Struve, 1992; ?*Echinocoeliopsis* Hamada, 1968.

Subfamily Eoreticulariinae Gourvennec, new subfamily

Diagnosis.—Smooth; with cardinal platform or septalium; ctenophoridium absent.

Discussion.—A mistake occurs in the translation to English of the work of

Nalivkin (1930:198) concerning *Eoreticularia*: “spines sometimes absent” should read “spines always absent” as is evident from the rest of the description. *Eoreticularia* is distinguished from both *Reticulariopsis* and *Reticularia* by the lack of spines. Havlíček (1971) notes the presence of radially aligned granules and the absence of marginal spines. The sections given by this author (1959:160, 163–164) show a septalium and delthyrial plate, but a ctenophoridium is absent.

Stratigraphic Range.—Silurian (Wenlock)—Upper Devonian (Frasnian).

Genera Included.—*Eoreticularia* Nalivkin in Frederiks, 1924; *Chnaurocoelia* Johnson, Boucot, and Murphy, 1976; *Vadum* Strusz, 1982.

Family Xenomartiniidae Havlíček, 1971

[Xenomartiniidae Havlíček, 1971, p. 24]

Diagnosis.—With ventral median septum.

Discussion.—In his conception of the family, Havlíček emphasized the lack of dental plates (1971:23). Here we would rather emphasize the presence of a ventral septum, which leads us to include the subfamilies Bojothyridinae and Quadriothyridinae and reject the *Obesaria* group. Close affinities exist between the Obesariinae and Xenomartiniidae, so that the latter probably were derived from the Obesariinae by acquisition of a ventral median septum.

Stratigraphic Range.—Upper Silurian–Middle Devonian.

Subfamily Xenomartiniinae Havlíček, 1971

[*nom. transl.* Gourvennec herein (*ex* Xeonmartiniidae Havlíček, 1971, p. 24)]

Diagnosis.—Smooth; lacking dental plates and ctenophoridium.

Discussion.—In 1953, Havlíček described the genus *Xenomartinia* (type species *X. monosepta*) including smooth forms with reticulate ornament and a ventral septum but lacking dental plates. In the same year Minato proposed the genus *Sinothyris* (type species *R. maureri*) with the following definition: “without dental plates but with median septum in the ventral valve.” This diagnosis corresponds to that of *Xenomartinia*, and thus the two genera would appear to be synonyms. On the other hand, Minato’s interpretation of the species *maureri* is clearly erroneous (Pitrat, 1965:H717), and this leads to some confusion in the definition of the genus *Sinothyris*. Pitrat placed *Sinothyris* in the synonymy of *Reticularia* with some doubt, but we now know that *Reticularia* possesses a myophragm or euseptoid rather than a true septum. The real question is one of priority. After inquiry, we have established that the work by Minato was published on September 30, 1953, while that of Havlíček was published in February 1953. Thus, *Sinothyris* is a junior synonym.

Stratigraphic Range.—Lower (Pragian)—Middle (Eifelian) Devonian.

Genera Included.—*Xenomartinia* Havlíček, 1953 [= *Sinothyris* Minato, 1953].

Subfamily Bojothyridinae Havlíček, 1990

[*nom. transl.* Gourvennec herein

(*ex* Bojothyrididae Havlíček, 1990, p. 186)]

Diagnosis.—With dental plates converging to median septum, commonly producing spondylium or spondylium-like structure.

Discussion.—Although it was first described as lacking dental plates (Havlíček, 1959:244), serial sections in *Quadriothyridina* apparently show tracks of rudimentary dental plates (or ridges) converging towards a septum. Thus, it is assigned here to the Bojothyridinae. On the other hand, the reduced size of these plates and the

apparently smooth cardinal process suggest strong affinities with the Xenomartiniinae. The same applies for *Uralospirifer* in which the dental plates are also reduced but seem somewhat more prominent than in *Quadrithyrina*. The two genera have an almost identical internal structure as pointed out by Havlíček (1959:142). *Uralospirifer* and *Altajella* are also very close externally, but the latter possesses a spondylium and crural plates and lacks an apical thickening of the shell. The genus *Altajella* can be seen as a possible ancestor of both the Bojothyridinae and Xenomartiniinae.

Stratigraphic Range.—Upper Silurian (Upper Ludlow)—Middle (Eifelian) Devonian.

Genera Included.—*Bojothyris* Havlíček, 1959; *Altajella* Kulkov, 1962; ?*Quadrithyrina* Havlíček, 1959; *Spondylothyris* Su, 1980.

Subfamily Quadrithyridinae Gourvennec, **new subfamily**

Diagnosis.—With divergent or subparallel dental plates.

Discussion.—The commissure of *Quadrithyrus* is sometimes strongly uniplicate. The crural plates are apparently lacking, but in some species (e.g., *Q. robusta*, *Q. orba*) small incipient crural plates are discernible on the bottom of the valve in serial sections. The redefinition of the genus by Boucot (1962) differs somewhat from the original definition. Some elements of this redefinition (e.g., the presence of crural plates) have been accepted in our diagnosis.

Stratigraphic Range.—Upper Silurian (Upper Wenlock)—Middle Devonian (Givetian).

Genus Included.—*Quadrithyrus* Havlíček, 1957.

Family Thomasariidae Cooper and Dutro, 1982 [Thomasariidae Cooper and Dutro, 1982, p. 102]

Diagnosis.—Small, hemipyramidal shells, with strong, long dental plates and a pair of conjunct apical plates. Dorsal interior with ctenophoridium, lacking crural plates. Surface with growth lines and fine spines.

Stratigraphic Range.—Upper Devonian (Frasnian).

Genus Included.—*Thomasaria* Stainbrook, 1945.

Family Elythidae Frederiks, 1924 [*nom. transl.* Pitrat, 1965, p. H721, ex Subfamily Elythinae Frederiks, 1924, p. 304]

Diagnosis.—Lateral slopes smooth or with low plications; fold and sulcus, if present, usually weakly developed; micro-ornament of fine biramous spines.

Discussion.—The development of biramous spines in this family is unique or synapomorphous and appears early in the history of the superfamily.

Stratigraphic Range.—Middle Devonian—Upper Permian.

Subfamily Elythinae Frederiks, 1924 [Subfamily Elythinae Frederiks, 1924, p. 304]

Diagnosis.—Spines biramous but not elaborate; ventral interior with dental adminicula and median ridge; dorsal interior with ctenophoridium.

Stratigraphic Range.—Lower Devonian—Lower Carboniferous.

Genera Included.—*Elita* Frederiks, 1918; *Kitakamithyris* Minato, 1951.

Subfamily Martinothyridinae Carter, **new subfamily**

Diagnosis. — Ventral interior with dental adminicula; ventral median ridge absent; spines elaborate.

Stratigraphic Range. — Lower Carboniferous–Lower Permian.

Genera Included. — *Martinothyris* Minato, 1953; *Latiplecus* Lee and Gu, 1976; *Orenburgella* Pavlova, 1969.

Subfamily Phricodothyridinae Caster, 1939

[*nom. correct.* Carter, herein,

pro Subfamily Phricodothyriinae Caster, 1939, p. 145]

Diagnosis. — Lacking dental adminicula and ventral median ridge; spines elaborate.

Stratigraphic Range. — Lower Carboniferous–Upper Permian.

Genera Included. — *Phricodothyris* George, 1932 [= ?*Bajkuria* Ustritsky, 1963; *Cond Rathyris* Minato, 1953; *Neophricodothyris* Likharev, 1934]; *Astegosia* Cooper and Grant, 1969; *Bullarina* Jing and Sun, 1981; *Nebenothyris* Minato, 1953; *Permophricodothyris* Pavlova, 1965.

Subfamily Toryniferinae Carter, **new subfamily**

Diagnosis. — Dental adminicula and low median ridge present; ctenophoridium absent; spines elaborate.

Stratigraphic Range. — Lower Carboniferous (Tournaisian)–Permian.

Genera Included. — *Torynifer* Hall and Clarke, 1893; *Plicotorynifer* Abramov and Solomina, 1970; *Spirolytha* Frederiks, 1924; *Stepanoviina* Zavadovsky, 1968; *Taimyrella* Ustritsky, 1963; *Toryniferella* Weyer, 1967.

Subfamily Anomaloriinae Cooper and Grant, 1976

[*nom. transl.* Carter, herein

(*ex* Family Anomaloriidae Cooper and Grant, 1976, p. 2260)]

Diagnosis. — Delthyrium covered with convex psuedodeltidium; ventral interior with converging thickened dental flanges that fuse apically; dorsal interior with notothyrial flanges fused to inner socket ridges that partially obscure sockets medially.

Stratigraphic Range. — Permian.

Genera Included. — *Anomaloria* Cooper and Grant, 1969; *Zhinania* Liang, 1990.

Order Spiriferinida Ivanova, 1972

[*nom. trans.* Carter and Johnson, herein

(*ex* Suborder Spiriferinidina Ivanova, 1972, p. 41)]

[= Order Spiriferinida Cooper and Grant, 1976, p. 2666]

Diagnosis. — Hingeline strophic; commonly transverse and biconvex; flanks ribbed, rarely smooth; ventral valve inflated and thicker than dorsal valve; ventral interarea commonly well developed; brachidium, where present, spiraliform, spiralia directed laterally or posterolaterally; jugum generally present; shell punctate.

Discussion. — Punctate spiriferids first appear near the Silurian–Devonian boundary as the distinctive small hemipyramidal genus *Cyrtina* Davidson. The growth form and complex internal structures of this genus indicate that it is morphologically highly specialized and may not reflect the ancestral stock from which this large group is derived. The immediate ancestors of the punctate spiriferids must have been strophic biconvex punctate orthids or impunctate spirifer-

ids with ventral sulcus and dorsal fold. Lacking recognizable antecedents, whether or not these close ancestors were punctate or impunctate cannot be demonstrated.

The Suborder Cyrtinidina comprises three superfamilies, the Cyrtinoidea, Suesioidea, and Spondylospiroidea, all characterized by having spondylia or related adductor-raising platforms. The Suessioidea were derived from the cyrtinoids in the Early Carboniferous, but the Carboniferous and Permian record is poor. The suessioids survived the Permian extinction event and flourished during the Middle and Late Triassic, when they became extinct. Sometime in the Early or very early Middle Triassic a stock of suessioids, the Spondylospiroidea, developed a unique crenulated hingeline. This short-lived group also disappeared in the Late Triassic.

The other punctate suborder, the Spiriferinidina, appeared in the Late Devonian as two distinct lineages, the superfamilies Pennospiriferinoidea and Syringothyridoidea, both derived from the cyrtinids at about the same time. These groups secondarily evolved a spiriferid growth form and discrete dental adminicula in the ventral valve. The syringothyridoids attained large size and survived until the Permian extinction event. The Pennospirinoidea developed a strong ventral median septum and became highly diverse throughout the Permian, but disappeared in the early Triassic, giving rise in the Middle Triassic to the last of the punctate superfamilies, the Spiriferinoidea. The latter group acquired its rounded growth form and reduced radial ornament, reminiscent of the reticularioids, by neoteny.

Stratigraphic Range.—Lower Devonian (Lower Lochkovian)—Lower Jurassic.

Suborder Cyrtinidina Carter and Johnson, **new suborder**

Diagnosis.—Lateral slopes plicate or smooth; ventral valve high, subconical or hemipyramidal in early forms, variable in later ones; delthyrium commonly covered in early genera, variably covered in late genera; ventral interior commonly with elevated adductor attachment structures.

Stratigraphic Range.—Lower Devonian—Lower Jurassic.

Superfamily Cyrtinoidea Frederiks, 1911

[*nom. transl.* Johnson, 1966, p. 177

(*ex* Cyrtininae Frederiks, 1911)]

Diagnosis.—Ventral valve hemipyramidal, with high interarea; dorsal valve flat or weakly convex; nonfimbriate and noncapillate; ventral median septum.

Stratigraphic Range.—Lower Devonian (basal Lochkovian)—Lower Carboniferous (Visean).

Family Cyrtinidae Frederiks, 1911

[*nom. transl.* Stehli, 1954, p. 350

(*ex* Cyrtininae Frederiks, 1911, p. 5)]

Diagnosis.—Stout, apically perforated deltidium; spondylium and divided trichorhinum; bilobed, commonly nonstriate cardinal process, but ctenophoridium may form in older growth stages.

Discussion.—We hypothesize that *Cyrtina*, the oldest genus of the Superfamily Cyrtinoidea, if not derived from an unknown punctate orthid or intermediate, was derived from one of the small impunctate Silurian genera of the Cyrtinopsinae in the Superfamily Delthyridoidea, possibly *Kozlowskiellina* Boucot, 1958. However, demonstrating homology between *Cyrtina* and impunctate taxa is not easy because general morphological similarity can indicate convergent or parallel evolution, as well as a genetic relationship.

Cyrtina became abundant at the beginning of the Devonian, already fully developed with endopunctate shell and tichorhinum. *Kozlowskiellina* is a small, lamellose, cyrtinaform genus with conjunct delthyrial plates pierced by an apical foramen. It has a ventral median septum and dental plates, and a bifid cardinal process in the dorsal valve. We assume that *Kozlowskiellina* could have given rise to *Cyrtinopsis* at about the same time that *Cyrtina* appeared, at the beginning of the Devonian. *Cyrtinopsis* differs from *Kozlowskiellina* by the presence of a spondylium pierced by a median septum and details of micro-ornament and is closer to *Cyrtina* in this way (Havlicek, 1959:144–145; Johnson, 1970:pl. 72, fig. 21–29). *Cyrtina* could have split off from the *Kozlowskiellina*–*Cyrtinopsis* phylogeny by the acquisition of an endopunctate shell structure and a tichorhinum.

Stratigraphic Range.—Lower Devonian (basal Lochkovian)–Lower Carboniferous (Visean).

Genera Included.—*Cyrtina* Davidson, 1858 [= *Spinocyrtina* Frederiks, 1916; *Cyrtinaellina* Frederiks, 1926; *Trochalocyrtina* Wright, 1975]; *Cyrtinaella* Frederiks, 1916; *Squamulariina* Frederiks, 1916 [= *Pyramidalia* Nalivkin, 1947]; *Tecnocyrtina* Johnson and Norris, 1972.

Family Komiellidae Johnson and Blodgett, 1993

[Family Komiellidae Johnson and Blodgett, 1993, p. 952]

Diagnosis.—Spondylium, or dental flanges and median septum not connected, lacking a tichorhinum; simple, nonstriate cardinal process; jugum sessile.

Discussion.—The name *Komiella* Barkhatova, 1970 (p. 62, footnote) is a *nomen nudum*.

Stratigraphic Range.—Lower Devonian (Emsian)–Upper Devonian (Frasnian).

Genus Included.—*Komiella* Liashenko, 1985.

Superfamily Suessioidea Waagen, 1883

[*nom. correct.* Carter, herein

(*pro* Superfamily Suessiacea Waagen, 1883) *nom. trans.* Pitrat, 1965, p. H675, *ex* Subfamily Suessiinae Waagen, 1883, p. 498]

Diagnosis.—Usually cyrtiniform; ventral valve usually hemipyramidal to subconical with high interarea; ventral median septum present, discrete dental adimicula absent; endopunctae or hemipunctae obscure in some genera.

Discussion.—In this superfamily there is an obvious relationship between the hemipyramidal or subconical growth form and internal structures of the ventral valve, namely the adductor-shortening structures such as the spondylium. The poor Paleozoic record of this superfamily hinders interpretation of relationships with the Cyrtinoidea from which the suessioids were derived, probably in the Lower Carboniferous. The Davidsoninidae are unique in this superfamily in being very large, in probably lacking crural processes and a brachidium, and in having hemipunctae. The Davidsoninidae are the only Carboniferous representatives of the Suessioidea, but if one invokes Dollo's Law they were probably not in the direct line of ancestry of the Laballidae, which first appear in the Upper Permian of China with normal brachidial structures intact.

Stratigraphic Range.—Lower Carboniferous (Visean)–Lower Jurassic.

Family Davidsoninidae Ivanova, 1972

[Family Davidsoninidae Ivanova, 1972, p. 41]

Diagnosis.—Lateral slopes ribbed; ventral interior with false spondylium com-

posed of median septum and high dental flanges; ventral adminicula absent; shell substance punctate, but punctae possibly not penetrating primary layer (hemipunctate); jugum and jugal processes absent; brachidium unknown, possibly absent.

Stratigraphic Range.—Lower Carboniferous (Visean–Namurian).

Genera Included.—*Davidsonina* Schuchert and LeVene, 1929; *Carbocyrtina* Ivanova, 1975.

Family Laballidae Dagus, 1962

[*nom. trans.* Dagus, 1965, p. 91,

ex Subfamily Laballinae Dagus, 1962, p. 49]

Diagnosis.—Cyrtiniform; spondylium bisected by high median septum.

Discussion.—This family appears cryptogenically with the genus *Eolaballa* Liao and Meng in the Upper Permian of China.

Stratigraphic Range.—Upper Permian–Upper Triassic.

Subfamily Laballinae Dagus, 1962

[Subfamily Laballinae Dagus, 1962, p. 49]

Diagnosis.—Fold and sulcus well defined; lateral slopes smooth or with one or two faint plicae; delthyrium open.

Stratigraphic Range.—Upper Permian–Upper Triassic.

Genera Included.—*Laballa* Moisseiev, 1962; *Eolaballa* Liao and Meng, 1986; *Pseudolaballa* Dagus, 1974.

Subfamily Spinolepismatininae Carter, **new subfamily**

Diagnosis.—Lateral slopes distinctly plicate; fold and sulcus smooth; micro-ornament densely spinulose.

Stratigraphic Range.—Upper Triassic.

Genera Included.—*Spinolepismatina* Dagus, 1974; *Klipsteinella* Dagus, 1974; *Klipsteinelloidea* Sun, 1981.

Subfamily Paralepismatininae Carter, **new subfamily**

Diagnosis.—Fold and sulcus poorly developed; entirely ribbed; micro-ornament absent.

Stratigraphic Range.—Middle Triassic (Anisian).

Genus Included.—*Paralepismatina* Yang and Xu, 1966.

Family Bittnerulidae Schuchert, 1929

[*nom. trans.* Carter, herein

(ex Subfamily Bittnerulinae Schuchert, 1929, p. 21)]

[=Subfamily Thecocyrtellinae Dagus, 1965, p. 105]

Diagnosis.—Cyrtiniform; dental adminicula and spondylium absent; ventral septum and dental flanges fused by apical callus or short transverse plate.

Stratigraphic Range.—Middle–Upper Triassic.

Subfamily Bittnerulinae Schuchert, 1929

[Subfamily Bittnerulinae Schuchert, 1929, p. 21]

Diagnosis.—Smooth or obscurely ribbed; fold and sulcus absent or very weak; delthyrium closed by convex deltidium.

Stratigraphic Range.—Middle–Upper Triassic.

Genera Included.—*Bittnerula* Hall and Clarke, 1895; *Leiolepismatina* Yang and Xu, 1966; *Thecocyrtella* Bittner, 1892; *Thecocyrtelloidea* Yang and Xu, 1966.

Subfamily Hirsutellinae Xu and Liu, 1983
[Subfamily Hirsutellinae Xu and Liu, 1983, p. 82]

Diagnosis.—Lateral slopes ribbed; fold and sulcus weakly to moderately developed; delthyrium open or partially occluded by various plates.

Stratigraphic Range.—Middle–Upper Triassic.

Genera Included.—*Hirsutella* Cooper and Muir-Wood, 1951; *Flabellocyrtia* Chorowicz and Termier, 1975; *Neocyrtina* Yang and Xu, 1966; *Spiriferinoides* Tokuyama, 1957.

Family Suessiidae Waagen, 1883
[*nom. trans.* Pitrat, 1965, p. H679
(ex Subfamily Suessiinae Waagen, 1883, p. 498)]

Diagnosis.—Entirely plicate; delthyrium open; dental adminicula and spondylium absent; large elongate hingeplate bearing adductors present.

Stratigraphic Range.—Lower Jurassic.

Genus Included.—*Suessia* Deslongchamps, 1855.

Superfamily Spondylospiroidea Hoover, 1991
[*nom. trans.* Carter, herein
(ex Family Spondylospiridae Hoover, 1991, p. 75)]

Diagnosis.—Spiriferiform to cyrtiniform; hingeline partially to completely crenulate; dental adminicula converging or forming spondylium; punctation well developed.

Discussion.—This compact group of 14 genera appeared cryptogenically in the Middle Triassic. Their unifying morphological character is the partially or completely crenulate hingeline. This articulatory structure has been termed “denticulate” by numerous authors but must be differentiated from the denticulate hingeline of the Spiriferoidea and Paleckelmanelloidea. In these groups the denticles consist of taleola-like rods embedded within secondary fibrous shell matter of the interareas. The crenulate teeth of the Spondylospiroidea lack “taleolae” and are similar in each valve and interlocking. This is a unique or possibly synapomorphic articular structure among the spiriferinids.

This group includes both wide-hinged “spiriferoid” genera and hemipyramidal “cyrtinoid” genera. Internally, there is a good spondylium in the “cyrtinoid” genera or converging dental adminicula in the “spiriferoid” genera. The cyrtiniform spondylium-bearing genera are considered here to be most primitive and to indicate derivation from the laballids. The spiriferiform wide-hinged genera seem likely to have been derived from a cyrtiniform ancestor with neotenous loss of the complete spondylium and concomitant extension of the hingeline.

Stratigraphic Range.—Upper Triassic.

Family Spondylospiridae Hoover, 1991
[Family Spondylospiridae Hoover, 1991, p. 75]

Diagnosis.—Cyrtiniform to globose; lateral slopes ribbed; spondylium bisected by high median septum; jugum complete, supported by sessile jugal net.

Stratigraphic Range.—Middle (Ladinian)–Upper Triassic (Rhaetian).

Subfamily Spondylospirinae Hoover, 1991
[Subfamily Spondylospirinae Hoover, 1991, p. 80]

Diagnosis.—Dental adminicula and ventral interarea complete, not pierced by paired pedicle foramina.

Stratigraphic Range.—Upper Triassic (Karnian–Rhaetian).

Genera Included.—*Spondylospira* Cooper, 1942; *Phenacozugmayerella* Hoover, 1991; *Vitimetula* Hoover, 1991; *Yanospira* Dagis, 1977; *Zugmayerella* Dagis, 1963.

Subfamily Dagyspiriferinae Hoover, 1991
[Subfamily Dagyspiriferinae Hoover, 1991, p. 77]

Diagnosis.—Globose to cyrtiniform; entirely ribbed; apex of spondylium and ventral interarea pierced by paired elongate foramina.

Stratigraphic Range.—Upper Triassic (Karnian–Norian).

Genera Included.—*Dagyspirifer* Hoover, 1991; *Pseudospondylospira* Hoover, 1991.

Family Rastelligeridae Carter, **new family**

Diagnosis.—Spiriferiform; usually transverse; fold and sulcus smooth; lateral slopes usually plicate; dental adminicula subparallel or convergent.

Stratigraphic Range.—Middle–Upper Triassic.

Subfamily Rastelligerinae Carter, **new subfamily**

Diagnosis.—Strongly transverse; cardinal extremities extended; lateral slopes strongly plicate; dental adminicula convergent or forming sessile spondylium.

Stratigraphic Range.—Middle (Ladinian)–Upper Triassic (Rhaetian).

Genera Included.—*Rastelligera* Hector, 1879; *Boreiospira* Dagis, 1974; *Psioi-diella* Campbell, 1968.

Subfamily Dentospiriferininae Carter, **new subfamily**

Diagnosis.—Cardinal extremities subangular to rounded; lateral slopes smooth or with few weak plicae; dental adminicula subparallel to convergent.

Stratigraphic Range.—Upper Triassic (Karnian–Norian).

Genera Included.—*Dentospiriferina* Dagis, 1965; *Canadospira* Dagis, 1972; *Orientospira* Dagis, 1965; *Psioidea* Hector, 1879.

Suborder Spiriferinidina Ivanova, 1972

[Suborder Spiriferinidina Ivanova, 1972, p. 41]

[=Suborder Spiriferinidina Cooper and Grant, 1976, p. 2666]

Diagnosis.—Subequally biconvex; ventral beak usually incurved; strong ventral median septum invariably present.

Discussion.—This suborder is presumed to have been derived from the cyrtinoid Family Komiellidae which had discrete dental adminicula in the Upper Devonian. Two distinct lineages appeared at this time. One formed the Pennospiriferinoidea with strong ventral median septum and leading to the highly successful radiation of similar genera in the Late Paleozoic and Triassic. The other lineage included large transverse genera bearing a strong delthyrial plate, the Syringothyridoidea. Although radically transformed internally, some of the advantages of the adductor-shortening structures of the cyrtinoid spondylium are retained in genera with a conical or hemipyramidal ventral valve, by the development of a simple high

median septum or large transverse delthyrial plate, respectively. In some moderately inflated, subequally biconvex syringothyridoid genera with low ventral interareas the delthyrial plate is lost, reflecting the lesser need for shortening the length of the adductors.

Stratigraphic Range.—Upper Devonian (Upper Famennian)—Lower Jurassic.

Superfamily Syringothyridoidea Frederiks, 1926

[*nom. correct.* Carter, herein (*pro* Syringothyridacea Frederiks, 1926

(*nom. imperf.*) *nom. trans.* Ivanova, 1972, p. 319,

ex Syringothyridae Frederiks, 1926, p. 411]]

Diagnosis.—Outline usually spiriferiform; moderately to strongly transverse; often strongly inequivalved; fold and sulcus invariably developed; lateral slopes with simple ribbing; micro-ornament consisting of fine short radial striae with fine elongate pustules or spinules arranged in quincunx between striae, producing textile-like appearance; dental adminicula present; cardinalia usually stout and wide; punctae highly variable in size, commonly sparsely and/or irregularly distributed.

Stratigraphic Range.—Upper Devonian (Upper Famennian)—Upper Permian.

Family Syringothrididae Frederiks, 1926

[*nom. correct.* Pitrat, 1965, p. H691 (*pro* Syringothyridae Frederiks, 1926

(*nom. imperf.*) *nom. transl.* Ivanova, 1959, p. 55,

ex Syringothyridae Frederiks, 1926, p. 411]]

Diagnosis.—Cardinal extremities subangular to slightly rounded; lateral slopes with moderately numerous simple ribs; interspaces narrow and subangular to moderately broad; fold and sulcus smooth medially; ventral interarea high to very high; perideltidial areas present.

Stratigraphic Range.—Upper Devonian (Upper Famennian)—Lower Permian.

Subfamily Syringothyridinae Frederiks, 1926

[*nom. correct.* Pitrat, 1965, p. H692

(*pro* Syringothyridae Frederiks, 1926, p. 411)]

Diagnosis.—Delthyrial plate and syrinx present.

Stratigraphic Range.—Upper Devonian (Upper Famennian)—Lower Permian.

Genera Included.—*Syringothyris* Winchell, 1863 [= *Syringopleura* Schuchert, 1910]; *Subansiria* Sahni and Srivastava, 1956.

Subfamily Septosyringothyridinae Massa, Termier, and Termier, 1974

[*nom. correct.* Legrand-Blain, 1974, p. 120,

pro Septosyringothyridae Massa, Termier, and Termier, 1974

(*nom. imperf.*) *nom. transl.* Carter, herein

(*ex* Septosyringothyridae Massa, Termier, and Termier, 1974, p. 168)]

Diagnosis.—Median septum and syrinx present in ventral valve.

Stratigraphic Range.—Lower Carboniferous.

Genera Included.—*Septosyringothyris* Vandercammen, 1955; *Histosyrinx* Massa, Termier, and Termier, 1974.

Subfamily Permasyrinxinae Waterhouse, 1986

[Subfamily Permasyrinxinae Waterhouse, 1986, p. 3]

Diagnosis.—Syrinx absent.

Discussion.—The validity of *Pseudosyringothyris* Frederiks is in doubt. Grigor'eva (1977) states that intensive collecting for topotypes of *P. karpinskii* has failed to produce specimens internally similar to Frederiks's description of the type specimens. The presence of perideltidial areas in *Primorewia* Likharev and Kotljar has not been confirmed. If they are truly lacking, then *Primorewia* should be reassigned to the Licharewiidae.

Stratigraphic Range.—Lower Carboniferous (Lower Tournaisian)—Upper Permian.

Genera Included.—*Permasyrinx* Waterhouse, 1983; *Asyrinx* Hudson and Sudbury, 1959 [= *Kungaella* Solomina, 1988]; *Asyrinxia* Campbell, 1957; *Cyrtella* Frederiks, 1924 [= *Punctocyrtella* Plodowski, 1968]; *Myodelthyrium* Thomas, 1985; ?*Primorewia* Likharev and Kotljar, 1978; ?*Pseudosyringothyris* Frederiks, 1916; *Pseudosyrinx* Weller, 1914; *Sulcicosta* Waterhouse, 1983; *Verkhotomia* Sokolskaya, 1963.

Family Dimegelasmidae Carter, new family

Diagnosis.—Cardinal extremities well rounded; ventral interarea low to moderately high; lateral slopes with few plications separated by broad rounded interspaces; sulcus sparsely plicate or costate; perideltidial areas present; syrinx absent; delthyrial plate small or absent; shell substance thin.

Stratigraphic Range.—Upper Devonian (Famennian)—Lower Carboniferous (Visean).

Genera Included.—*Dimegelasma* Cooper, 1942 [= *Doescherella* Abramov and Grigor'eva, 1987]; *Guilinospirifer* Xu and Yao, 1988; *Zeugopleura* Carter, 1988.

Family Licharewiidae Slyusareva, 1958

[*nom. trans.* Solomina, 1988, p. 44

(*ex* Licharewiinae Slyusareva, 1958, p. 582)]

Diagnosis.—Perideltidial areas absent; syrinx absent; moderate to thick callus deposits in ventral umbonal region commonly present.

Discussion.—The presence or absence of perideltidial areas in *Pyramidathyris* Hu, *Tumarinia* Solomina and Grigor'eva, and *Tuotalania* Hu has not been demonstrated. The presence of such areas in any of these genera would require transfer to the Family Syringothyrididae.

Stratigraphic Range.—Upper Carboniferous—Upper Permian.

Genera Included.—*Licharewia* Einor, 1939 [= *Rugulatia* Sokolskaya, 1952]; *Olgardia* Grigor'eva, 1977; *Orulganina* Solomina and Cherniak, 1961; *Penzhinella* Solomina, 1985; *Permospirifer* Kulikov, 1950; ?*Pyramidathyris* Hu, 1983; ?*Tumarinia* Solomina and Grigor'eva, 1973; ?*Tuotalania* Hu, 1983.

Superfamily Pennospiriferinoidea Dagens, 1972

[*nom. trans.* Carter, herein

(*ex* Subfamily Pennospiriferininae Dagens, 1972, p. 36)]

Diagnosis.—Spiriferiform to cyrtiniform; ventral interarea usually low or only moderately high; lateral slopes ribbed; dental adminicula and median septum discrete; punctae well developed, usually densely spaced.

Stratigraphic Range.—Upper Devonian (Upper Famennian)—Lower Jurassic.

Family Punctospiriferidae Waterhouse, 1975

[*nom. correct.* Carter, herein,

(*pro* Family Punctospiriferinidae Waterhouse, 1987, p. 44;

nom. trans. Waterhouse 1983 or 1987, *ex* Subfamily
Punctospiriferinae Waterhouse, 1975, p. 17]]

Diagnosis.—Usually transverse; fold and sulcus narrow, weakly to moderately developed; dental adminicula short, subparallel to slightly divergent; micro-ornament capillate and usually regularly lamellose or subimbricate.

Discussion.—The faintly capillate micro-ornament in *Yangkongia* Xu and Liu is very poorly preserved and may in fact be an artifact of preservation. If so, reassignment would be necessary.

The earliest genus in this superfamily, *Ziganella* Nalivkin, has a low ventral median septum or ridge and normal fold-sulcus. This punctospiriferid genus is believed to have been derived from the Komiellidae or some intermediate ancestor within this lineage.

Stratigraphic Range.—Upper Devonian (Upper Famennian)—Middle Triassic.

Genera Included.—*Punctospirifer* North, 1920; *Alipunctifera* Waterhouse, 1975; *Lamnaespina* Waterhouse, 1976; *Liriplica* Campbell, 1961; *Pustulospiriferina* Waterhouse, 1983; ?*Yangkongia* Xu and Liu, 1983; *Ziganella* Nalivkin, 1960.

Family Spiropunctiferidae Carter, **new family**

Diagnosis.—Cardinal extremities well rounded; fold and sulcus plicate; micro-ornament absent.

Stratigraphic Range.—Lower Carboniferous (Upper Visean)—Upper Permian.

Genera Included.—*Spiropunctifera* Ivanova, 1971; *Genuspirifer* Liang, 1990.

Family Reticulariinidae Waterhouse, 1975

[*nom. trans.* Waterhouse, 1983, p. 138,

ex Subfamily Reticulariininae Waterhouse, 1975, p. 15]

Diagnosis.—Outline transverse; cardinal extremities usually extended, rarely rounded; fold and sulcus narrow, usually well delimited; sulcus smooth or with weak median rib; dental adminicula divergent; micro-ornament of coarse hollow spines.

Stratigraphic Range.—Lower Carboniferous (Upper Visean)—Upper Permian.

Genera Included.—*Reticulariina* Frederiks, 1916; *Altiplecus* Stehli, 1954; *Gjelspinifera* Ivanova, 1975; *Spinuliplica* Campbell, 1961.

Family Paraspiriferinidae Cooper and Grant, 1976

[Family Paraspiriferinidae Cooper and Grant, 1976, p. 2729]

Diagnosis.—Outline transversely subelliptical; cardinal extremities well rounded; fold and sulcus usually well delimited; dental adminicula short, usually divergent; micro-ornament regularly and finely lamellose, with lamellae bearing fine hair-like spinules in some genera.

Stratigraphic Range.—?Lower Carboniferous (Upper Visean), Upper Carboniferous—Upper Permian.

Genera Included.—*Paraspiriferina* Reed, 1944; *Callispirina* Cooper and Muir-Wood, 1951; *Lamnipllica* Waterhouse and Rao, 1989; *Polystylus* Klets, 1993; *Yaoniella* Waterhouse, 1983; *Zaissania* Sokoskaya, 1968.

Family Crenispiriferidae Cooper and Grant, 1976

[Family Crenispiriferidae Cooper and Grant, 1976, p. 2709]

Diagnosis.—Outline usually transversely subelliptical to subtrigonal; fold and sulcus usually narrow and poorly to moderately delimited; lateral slopes with few

strong lateral plicae and subimbricate growth varices; dental adminicula very short; micro-ornament finely pustulose.

Discussion.—*Tulungospirifer* Ching and Sun is tentatively assigned here on the basis of its growth form. Its micro-ornament differs from other genera in this family in having radial grooves and spinules.

Stratigraphic Range.—Lower Carboniferous (Upper Chesterian)—Upper Triassic.

Genera Included.—*Crenispirifer* Stehli, 1954; *Lancangjiangia* Jin and Fang, 1977; *Metriolepis* Cooper and Grant, 1976; *Pseudospiriferina* Young and Xu, 1966; *Spiriferellina* Frederiks, 1924 [= *Tylotoma* Grabau, 1934]; *Sulcispiriferina* Waterhouse and Gupta, 1981; ?*Tulungospirifer* Ching and Sun, 1976.

Family Sarganostegidae Cooper and Grant, 1976

[Family Sarganostegidae Cooper and Grant, 1976, p. 2743]

Diagnosis.—External surface with quincunially arranged very coarse punctae; micro-ornament absent.

Stratigraphic Range.—Middle–Upper Permian.

Genus Included.—*Sarganostega* Cooper and Grant, 1969.

Family Balatonospiridae Dagus, 1974

[*nom. trans.* Carter, herein,

ex Subfamily Balatonospirinae Dagus, 1974, p. 137]

[=Subfamily Nudispiriferinae Xu and Liu, 1983]

Diagnosis.—Outline transversely subelliptical to subquadrate or subpentagonal; fold and sulcus poorly developed; entire surface usually ribbed.

Stratigraphic Range.—Middle–Upper Triassic.

Subfamily Yalonginae Carter, **new subfamily**

Diagnosis.—Dental adminicula discrete.

Stratigraphic Range.—Middle Triassic.

Genera Included.—*Yalongia* Xu and Liu, 1983; *Aequispiriferina* Yang and Yin, 1962; *Sinuocostella* Xu and Liu, 1983.

Subfamily Balatonospirinae Dagus, 1974

[Subfamily Balatonospirinae Dagus, 1974, p. 137]

Diagnosis.—Dental adminicula reduced or absent; dental flanges and median septum fused by transverse plate or callus.

Stratigraphic Range.—Middle (Anisian)—Upper (Karnian) Triassic.

Genera Included.—*Balatonospira* Dagus, 1974; *Dinarispira* Dagus, 1974; *Koeveskallina* Dagus, 1965; *Nudispiriferina* Yang and Xu, 1966; *Tylospiriferina* Xu, 1978.

Family Pennospiriferinidae Dagus, 1972

[*nom. trans.* Carter, herein,

ex Subfamily Pennospiriferininae Dagus, 1972, p. 36]

Diagnosis.—Transverse, usually with angular or extended lateral extremities; dental adminicula subparallel or converging; micro-ornament absent.

Stratigraphic Range.—Upper Carboniferous–Upper Triassic (Karnian), ?Lower Jurassic.

Subfamily Pennospiriferinae Dagus, 1972
[Subfamily Pennospiriferinae Dagus, 1972, p. 36]

Diagnosis. — Fold and sulcus smooth; dental adminicula converging, fused with median septum by thick callus.

Discussion. — The micro-ornament of *Callospiriferina* Rousselle, if any, is poorly known. Furthermore, the growth form of this genus differs substantially from that of the type genus.

Stratigraphic Range. — Middle Triassic (Ladinian)–?Lower Jurassic.

Genera Included. — *Pennospiriferina* Dagus, 1965; ?*Callospiriferina* Rousselle, 1977.

Subfamily Punctospirellinae Dagus, 1974
[Subfamily Punctospirellinae Dagus, 1974, p. 135]
[=Family Xestotrematidae Cooper and Grant, 1976, p. 2748]

Diagnosis. — Fold and sulcus smooth or weakly ribbed; dental adminicula discrete, usually short, not converging.

Discussion. — This long-ranging subfamily, if it proves to be monophyletic, is probably the ancestral stock for the other Triassic families in this superfamily.

Stratigraphic Range. — Upper Carboniferous–Middle Triassic.

Genera Included. — *Punctospirella* Dagus, 1974; *Arionthia* Cooper and Grant, 1976; *Laioporella* Ivanova, 1975; *Xestotrema* Cooper and Grant, 1969 [= *Mucrospiriferinella* Waterhouse, 1982].

Family Lepismatinidae Xu and Liu, 1983
[Family Lepismatinidae Xu and Liu, 1983, p. 82]

Diagnosis. — Cyrtiniform or globose; lateral slopes ribbed; fold and sulcus well developed; delthyrium open; dental adminicula discrete.

Stratigraphic Range. — Middle Triassic–Lower Jurassic.

Subfamily Lepismatininae Xu and Liu, 1983
[*nom. trans.* Carter, herein,
ex Family Lepismatinidae Xu and Liu, 1983, p. 82]

Diagnosis. — Fold and sulcus smooth; micro-ornament of dense spinules; cardinalia sessile.

Stratigraphic Range. — Middle–Upper Triassic.

Genera Included. — *Lepismatina* Wang, 1955 [= *Costispiriferina* Dagus, 1974]; *Altoplicatella* Xu and Liu, 1983; *Pseudolepismatina* Ching and Sun, 1976.

Subfamily Pseudocyrtininae Carter, **new subfamily**

Diagnosis. — Fold and sulcus smooth; cardinalia supported by short median septum; micro-ornament absent.

Stratigraphic Range. — Upper Triassic.

Genera Included. — *Pseudocyrtina* Dagus, 1962; *Bolilaspirifer* Sun, 1981.

Subfamily Dispiriferinae Carter, **new subfamily**

Diagnosis. — Entirely ribbed; no dorsal septum.

Stratigraphic Range. — Middle Triassic–Lower Jurassic.

Genera Included. — *Dispiriferina* Siblik, 1965; *Qingyenina* Yang and Xu, 1966.

Superfamily Spiriferinoidea Davidson, 1884

[*nom. correct.* Carter, herein (*pro* Superfamily Spiriferinacea Davidson, 1884
(*nom. imperfect.*) *nom. trans.* Ivanova, 1959, p. 57,
ex Subfamily Spiriferininae Davidson, 1884, p. 354)]

Diagnosis.—Reticulariiform, subequally biconvex; cardinal extremities well rounded; ventral beak incurved; fold and sulcus usually weakly developed; lateral slopes smooth or obscurely ribbed, rarely with moderately developed ribbing.

Discussion.—The growth form, internal morphology, and micro-ornament of this superfamily strongly suggest that it was derived from some member of the Family Paraspiriferinidae.

Stratigraphic Range.—Middle Triassic–Lower Jurassic.

Family Spiriferinidae Davidson, 1884

[*nom. trans.* Ivanova, 1959, p. 57
(ex Subfamily Spiriferinidae Davidson, 1884, p. 354)]

Diagnosis.—Lateral slopes smooth or obscurely ribbed.

Stratigraphic Range.—Middle Triassic–Lower Jurassic.

Subfamily Spiriferininae Davidson, 1884

[Subfamily Spiriferinidae Davidson, 1884, p. 354]
[=Subfamily Spiriferellinae Paeckelmann, 1932, p. 25,
pro Spiriferininae Schuchert, 1929, p. 21]

Diagnosis.—Reticulariiform; dental adminicula discrete.

Stratigraphic Range.—Middle Triassic–Lower Jurassic.

Genera Included.—*Spiriferina* Orbigny, 1847 [= *Liospiriferina* Rouselle, 1977]; *Calyptoria* Cooper, 1989 [= *Cingolospiriferina* Pozza, 1992]; *Mentzelioides* Dagus, 1974; *Qinghaispiriferina* Sun and Ye, 1982; *Triadispira* Dagus, 1961; *Viligella* Dagus, 1965.

Subfamily Paralaballinae Carter, **new subfamily**

Diagnosis.—Cyrtniiform; fold and sulcus weakly developed; ornament absent; dental adminicula discrete, thin, short, subparallel.

Stratigraphic Range.—Upper Triassic.

Genus Included.—*Paralaballa* Sun, 1981.

Subfamily Mentzeliinae Dagus, 1974

[Subfamily Mentzeliinae Dagus, 1974, p. 138]

Diagnosis.—Dental adminicula absent.

Stratigraphic Range.—Middle–Upper Triassic.

Genera Included.—*Mentzelia* Quenstedt, 1871; *Madoia* Sun and Ye, 1982; *Paramentzelia* Xu, 1978.

Subfamily Tethyspirinae Carter, **new subfamily**

Diagnosis.—Spondylium present.

Stratigraphic Range.—Middle (Ladinian)–Upper (Karnian?) Triassic.

Genera Included.—*Tethyspira* Siblik, 1991; *Spondylospiriferina* Dagus, 1972.

Family Sinucostidae Xu and Liu, 1983

[*nom. trans.* Carter, herein,
ex Subfamily Sinucostinae Xu and Liu, 1983, p. 112]

Diagnosis.—Lateral slopes ribbed; dental adminicula discrete.
Stratigraphic Range.—Middle–Upper Triassic, ?Lower Jurassic.

Subfamily Sinucostinae Xu and Liu, 1983
 [Subfamily Sinucostinae Xu and Liu, 1983, p. 112]

Diagnosis.—Dorsal septum absent.

Stratigraphic Range.—Middle–Upper Triassic, ?Lower Jurassic.

Genera Included.—*Sinucosta* Dagis, 1963 [= *Guseriplica* Dagis, 1963]; *Mentze-liopsis* Trechmann, 1918; *Qispiriferina* Xu and Liu, 1983.

Subfamily Jiangdaspiriferinae Carter, **new subfamily**

Diagnosis.—With dorsal median septum.

Stratigraphic Range.—Upper Triassic.

Genus Included.—*Jiangdaspirifer* Chen, Rao, Zhou, and Pan, 1986.

Suborder uncertain
 Superfamily uncertain
 Family uncertain

Genus Included.—*Plicatosyrinx* Minato, 1952.

REJECTED FROM THE SPIRIFERS

Genera Included.—*Guangshunia* Xian 1978 [possible stringocephalid]; *Iliella* Rukavishnikova 1980 [Ashgill, not an *Eospirifer*]; *Plectospirifer* Grabau, 1931 [its type species is a synonym of *Athyrisina squamosa* Hayasaka, type species of *Athyrisina*]; *Pustulatia* Cooper 1956 [possible anoplotheacid]; *Xerxespirifer* Cocks 1979 [rhynchonellid or leptocoeliid].

ACKNOWLEDGMENTS

Johnson's research was supported by National Science Foundation Grant EAR-9204772.

APPENDIX

Boucot (1973:39–61; 1975:369–370) used the term “ctenophoridium” for the striate site of dorsal diductor attachment in some spiriferid brachiopod genera, but did not define the term. We remedy that oversight here and call attention that “ctenophoridium” will appear as an accepted usage in the glossary of the forthcoming revision of the brachiopod Treatise. Krans (1965:pl. 16) illustrated thin sections of the ctenophoridium, which he referred to as a cardinal process of *Cyrtospirifer* and an unidentified genus.

ctenophoridium.—Striated or comb-like site of dorsal diductor muscle attachment situated on floor of notothyrial cavity or bifid on hinge plates, but not elevated on a shaft-like cardinal process.

LITERATURE CITED

To include here every dated citation given above would require the editors to print many pages of text in addition to an already long paper. Therefore, we exclude references for the taxonomic units and list here only those papers cited in the text. Readers who wish to obtain citations for a particular taxon may call, write, or e-mail Carter. Carter's e-mail address is: JLC4@VMS.CIS.PITT.EDU; telephone (412) 622-3263.

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